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RELATIVE ABUNDANCE AND HABITAT RELATIONSHIPS OF *Clethrionomys rutilus* IN THE SOUTH-CENTRAL YUKON TERRITORY

by

© STEPHEN S. BEARE

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled **RELATIVE ABUNDANCE AND HABITAT RELATIONSHIPS OF** *Clethrionomys rutilus* **IN THE SOUTH-CENTRAL YUKON TERRITORY** submitted by **STEPHEN S. BEARE** in partial fulfilment of the requirements for the degree of **MASTER OF SCIENCE.**

...W.A. Fuller...

Supervisor

...

...

...

Date...June 11/84.....

DEDICATION

This thesis is dedicated to my parents,
who instilled within me a true appreciation
of wildlife and wilderness.

ABSTRACT

During a study of small mammals near km 42 on the South Canol Road, south-central Yukon, 1142 animals of 14 species were captured in 23,940 trap nights in 1979, 1980 and 1981. The northern red-backed vole (*Clethrionomys rutilus*), which inhabited five habitat types, constituted 82.3% of the total catch and was clearly the numerically dominant species. The meadow vole (*Microtus pennsylvanicus*), second in abundance, accounted for 3.6% of the total captures, with 12 species comprising the remaining 14.1%. *Clethrionomys rutilus* abundance varied among seasons, years and habitats, but there was little evidence of a multiannual cycle. Various demographic parameters were examined in an attempt to determine the habitat preferred by *C. rutilus*. Although abundance differed among habitats, body weight, body length and condition showed no significant differences among habitats. Young of the year voles were predominantly in age class I in 1979 and age class II in 1980, presumably as a result of an earlier onset of breeding in the second year. Otherwise, age structure of the samples was similar across habitats. Overwintered females had more and significantly larger litters than young of the year females, but there was no significant difference in reproductive output per female between habitats.

Two of the 5 habitats (Habitats II and III) appeared to be the most favourable with reference to both animal abundance and quality, as measured by the various demographic parameters. Protection from predation is assumed to be the primary reason for greater vole abundance in sites with more cover. Habitats II and III possessed much debris and the plant species afforded ground cover for the resident voles.

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I would like to take this opportunity to express special thanks to my supervisor, Dr. W.A. Fuller, for his assistance in planning this study, guidance throughout the long and winding road, and his tolerance and patience through endless rereads of my version of scientific English. In addition to the scientific knowledge learned from him, was the insight I acquired dealing with the bush and The North. Both forms of knowledge are invaluable and shall influence me until I hand in my dinner pail. I feel very fortunate to have had him as a supervisor, and benefited greatly from his input.

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A debt of gratitude is owed my two very capable and unfailing "Textformers", Heidi Zwickel and Tracy Marchant, who graciously and cheerfully gave of their time and expertise to type this manuscript critically and efficiently and to come to grips with the computerized nemesis. I cannot thank them enough for the hours they spent at the keyboard, and the wits they possessed for actually getting the written word out of the computer once it was in.

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Finally, I owe a debt of gratitude to the multitude of little critters who, albeit not voluntarily, paid the supreme sacrifice for science. Truly without them this would have been a completely different project than the one presented before you.

Table of Contents

Chapter	Page
DEDICATION	iv
ABSTRACT	v
ACKNOWLEDGMENTS	vii
LIST OF TABLES	xii
LIST OF FIGURES	xvi
LIST OF APPENDICES	xvii
INTRODUCTION	1
STUDY AREA	3
METHODS	9
SMALL MAMMAL TRAPPING	9
VEGETATION SURVEY	19
RESULTS	23
VEGETATION ANALYSIS	23
SPECIES DIVERSITY	31
RELATIVE ABUNDANCE OF *Clethrionomys rutilus*	35
SEX RATIOS	42
AGE STRUCTURE	45
BIOMASS	50
BODY WEIGHT AND LENGTH	54
CONDITION	64
REPRODUCTION	66
LIVE TRAPPING	74
DISCUSSION	77
CRITERIA FOR HABITAT PREFERENCE	77
THE "IDEAL" HABITAT	83

DEMOGRAPHY OF *C. rutilus* WITH REGARD TO HABITAT RELATIONSHIPS 93

CONCLUSION 101

TABLES 104

LITERATURE CITED 156

APPENDICES 169

LIST OF TABLES

Table		Page
1	Approximate dates of disappearance of snow and first snow on the habitats of the study area	105
2	Climatological data for the summer field seasons of 1979 and 1980	106
3	Dates on which snap-traps were set	107
4	Length of live-trapping transects with number of traps per habitat type	108
5	Area of habitat types and percentage of live-trapping effort by habitat	109
6	Dates on which live-traps were set	110
7	Marked animals removed by snap-trapping the live-trap sites	111
8	Summary of the discriminant function analysis showing the significance of the variables chosen and the percent variance explained by the functions	112
9	Habitat type description for the study area from data from two vegetation plots per habitat	113
10	Estimated percent cover of trees observed by habitat type	114
11	Mean percent cover of shrubs by habitat type	115
12	Mean percent cover of herbs by habitat type	117

13 Mean percent cover of mosses and lichens by habitat type.....120

14 Number of individuals, number of species, diversity and evenness of species captured in the spring trapping sessions.....122

15 Number of individuals, number of species, diversity and evenness of species captured in the fall trapping sessions.....123

16 Species diversity and evenness of small mammals captured in the study area during spring trapping.....124

17 Species diversity and evenness of small mammals captured in the study area during fall trapping.....125

18 The degree of difference between habitat types during spring trapping.....126

19 The degree of difference between habitat types during fall trapping 127

20 rD values and percentage of total rD attributed to various pairs of habitats.....128

21 Results of the Student-Newman-Keuls procedure for the fall mean captures per trapline of *C. rutilus*.....129

22 Results of the Student-Newman-Keuls procedure for the fall mean captures of *C. rutilus* males, in 150 T.N.....130

23 Results of the Student-Newman-Keuls procedure for the fall mean captures of *C. rutilus* females, in 150 T.N.....131

24 Results of the Student-Newman-Keuls procedure for the fall 1979 and 1980 mean trapline captures of *C. rutilus*.....132

25 Proportion of males caught in the fall trapping sessions.....133

26 Proportion of age classes of fall-captured *C. rutilus*.....134

27 Proportion of age class (n) in samples of *C. rutilus* in fall snap-trapping.....135

28 The Student-Newman-Keuls procedure for the fall (1979 and 1980) biomass of *C. rutilus*, following a 1-Way Anova 136

29 The Student-Newman-Keuls procedure for the spring body length of *C. rutilus*, following an analysis of covariance.....137

30 Mean ± S.E. body lengths of the combined 1979 and 1980 fall sample of late cohort *C. rutilus*.....138

31 Mean ± S.E. body lengths of immature and mature early cohort *C. rutilus* captured in the fall 1979 and 1980 trapping sessions.....139

32 Mean condition factor ± S.E. for the combined 1979 and 1980 fall sample of the late cohort *C. rutilus*.....140

33 Mean condition factor ± S.E. for the combined 1979 and 1980 fall sample of the early cohort male *C. rutilus*.....141

34 Mean condition factor ± S.E. for the combined 1979 and 1980 fall sample of the early cohort female *C. rutilus*.....142

35 The Student-Newman-Keuls procedure for the condition factor of mature and immature early cohort female *C. rutilus*, following a 2-Way Anova.....143

36 Dates of reproductive activities of female *C. rutilus* calculated by back-dating.....144

37 Pregnancy rates in the fall 1979 and 1980 combined samples of *C. rutilus* 145

38 Mean litter size ± S.E. of OW *C. rutilus* in spring trapping 1979, 1980 and 1981.....146

39 The Student-Newman-Keuls procedure for the mean number of embryos in the last litter of age class III *C. rutilus*, following a 1-Way Anova.....147

40 Mean litter size ± S.E., mean number of litters and output per female and per 100 T.N. of *C. rutilus* captured in the combined 1979 and 1980 fall trapping sessions, by age and habitat.....148

41 Weighted average output of embryos per female in the combined 1979 and 1980 fall sample, by age and habitat.....151

42 Proportion of mature males by age class.....152

43 Summary of *C. rutilus* live-trapping results from 1979 and 1980.....153

44 Proportion of males, by age class, of *C. rutilus* removed from the live-trap lines during the seventh rota, 1980.....154

45 Habitat ranking with regard to those demographic variables of *C. rutilus* significantly different among habitats.....155

LIST OF FIGURES

Figure		Page
1	Map of Yukon showing location of study area	4
2	Age classes of trees in the Evelyn Creek study area, Yukon Territory	6
3	Height classes of trees in the Evelyn Creek study area, Yukon Territory	7
4	Position of snap-trap lines by habitat	10
5	Catch per 100 trap-nights of small mammals in the five habitat types, 1979	37
6	Catch per 100 trap-nights of small mammals in the five habitat types, 1980	39
7	Proportion of age classes of *C. rutilus* captured on the supplemental trap-lines	47
8	Mean spring (1979, 1980 and 1981 combined) and fall (1979 and 1980 combined) biomass of *C. rutilus* by habitat	53
9	Mean body weights ± S.E. and range of mature *C. rutilus* (early cohort) from the 1979 and 1980 fall trapping sessions	57
10	Mean body weights ± S.E. and range of immature *C. rutilus* (early cohort) from the 1979 and 1980 fall trapping sessions	59
11	Mean body weights ± S.E. and range of age class I *C. rutilus* (late cohort) from the 1979 and 1980 fall trapping sessions	62

LIST OF APPENDICES

Appendix		Page
1	Standard vegetation form	171
2	Vegetation observation card	176
3	Mean catch per 100 T.N. per trapline of *C. rutilus* on 4 traplines in each habitat found in the study area during spring and fall trapping	177
4	Two-Way Anova for the fall 1979 and 1980 trapline captures of *C. rutilus*	178
5	Replicated Goodness of Fit Test for the spring sex ratios	179
6	Proportion of males, based on index-trapping of habitats, for the spring trapping sessions	180
7	Sex ratios and replicated Goodness of Fit results for the summer 1980 captures of *C. rutilus* pooled over five habitats	181
8	Replicated Goodness of Fit Test for the sex ratios of *C. rutilus* removed from the live-trap lines in 1980	182
9	Two-Way Anova for the biomass of the 1979, 1980 and 1981 spring trapline captures of *C. rutilus*	183
10	Three-Way Anova for the biomass of the 1979 and 1980 fall trapline captures of *C. rutilus*	184
11	Analysis of Covariance for the body weights of spring-caught *C. rutilus*	185

12 Two-Way Anova for the body weights of the 1979 and 1980 combined fall samples of mature and immature male *C. rutilus*.....188

13 Two-Way Anova for the body weights of the 1979 and 1980 combined fall samples of mature and immature female *C. rutilus*.....189

14 Two-Way Anova for the body weights of the 1979 and 1980 combined fall samples of late cohort *C. rutilus*.....190

15 Analysis of Covariance for the body lengths of spring-caught *C. rutilus*.....191

16 Two-Way Anova for the body lengths of the 1979 and 1980 combined fall samples of mature and immature male *C. rutilus* (early cohort).....192

17 Two-Way Anova for the body lengths of the 1979 and 1980 combined fall samples of mature and immature female *C. rutilus* (early cohort).....193

18 Two-Way Anova for the condition factor of mature and immature early cohort female *C. rutilus* in the combined 1979 and 1980 fall samples.....194

19 Two-Way Anova for the number of litters produced by the mature age classes of *C. rutilus* in the fall trapping of 1979 and 1980.....195

INTRODUCTION

Few detailed surveys of small mammals have been undertaken in the south-central Yukon. A study was conducted by Krebs and Wingate (1976) in south-western Yukon, and other authors (Rand, 1945; Baker, 1951; Cameron, 1952; Banfield, 1974; Youngman, 1975) have discussed small mammal distributions in other regions of the territory.

This study was initiated by the Yukon Wildlife Branch in an attempt to gain more information about the prey base of the pine marten (*Martes americana*), which has always been an important part of the Yukon fur harvest (Archibald and Russell, 1979). The initial purpose of the study was to determine the relative abundance and diversity of prey species in each of several habitat types. The objective was later broadened to include a study of habitat preference by the most abundant murid, *Clethrionomys rutilus*, present on the study site. Differences in habitat quality may result in differential habitat use or preference by this species of small mammal, and in addition may be reflected not only by abundance but also by "animal quality". To this end, various indices of animal quality (eg. body weight, body length, condition factor and reproductive output) were considered in an attempt to determine if habitat differences had any effect on animal quality.

Five distinct vegetation or habitat types in the boreal coniferous forest were defined and delineated by the Yukon Wildlife Branch for both marten and small mammal studies. The term "habitat type" has been used in this context to include only vegetation parameters and does not include other biotic or abiotic factors which influence the distribution and abundance of the resident flora and fauna.

Use of plant communities by small rodents may be influenced by a number of factors related to vegetation structure. A variety of other factors are no doubt involved in determining the distribution and abundance of a particular species of small rodent, for example the processes of dispersal and competition (Krebs, 1978), but this study is concerned only with the analysis of vegetation structure. Vegetation composition and structure is of major significance for certain species of small mammals, as several studies have shown (Findley, 1951; Quast, 1954; Wecker, 1963; Zimmerman, 1965; Grant, 1971; Miller and Getz, 1972; 1973; Kirkland and Griffin, 1974; Douglass, 1976; Drickamer, 1976; Meserve, 1976(b); Dueser and Shugart, 1978; Randall, 1978). Available moisture, vegetation density and habitat complexity, among others, are intricately involved in determining the abundance and diversity of small mammal communities.

STUDY AREA

The study area is on the north-facing slope of "Mount Mouse" in the Big Salmon Range at approximately 60° 45' N., 133° 15' W. It is accessible by way of a 6 km trail that leaves the South Canol Road at Kilometre Post 42 (Fig. 1). Its area is approximately 14 km² and it extends from just below tree line in the south (elevation 1220 m) to Evelyn Creek in the north (elevation 850 m).

Across the width of the study area eight transects were cut at intervals of 0.8 km. The cut-lines, averaging 2 km in length (range 1.5 - 2.7 km), provided access within the study area for the placement of both live and snap-traps.

The study area, which lies within the region of the boreal forest in the Central Yukon section (B.26b) (Rowe, 1972), contains stands of *Pinus contorta* (lodgepole pine), *Abies lasiocarpa* (subalpine fir), *Picea glauca* (white spruce) and *Picea mariana* (black spruce). *Pinus contorta* and *Picea glauca* are the dominant forest types on well-drained soil of the valleys and lower slopes, whereas a dense scrub of *A. lasiocarpa* extends up the mountain slopes to an elevation of approximately 1500 m (5000 feet) (Porsild, 1951).

All forests along the Canol Road, except those growing on moist north and east slopes and near timberline, have

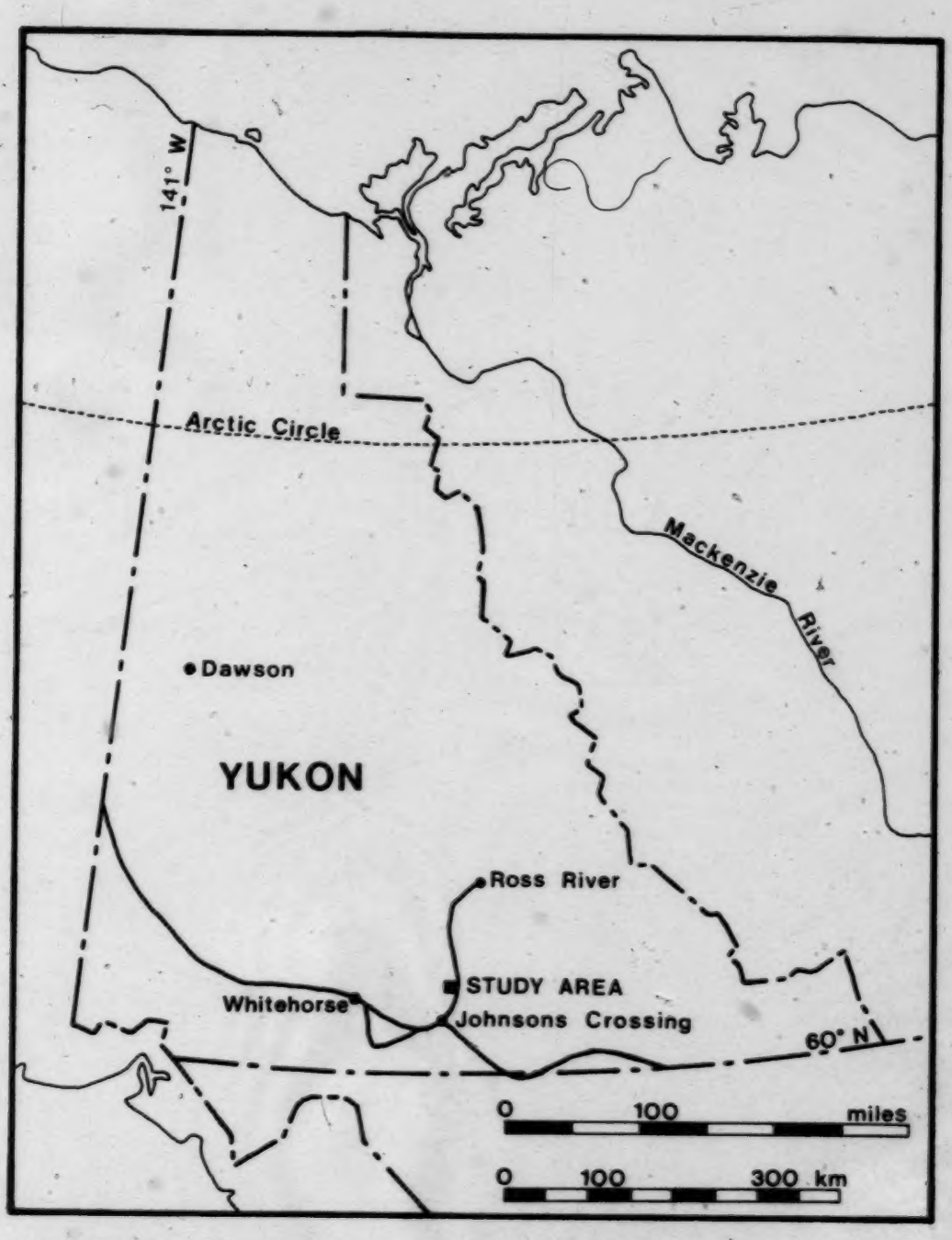


FIGURE 1: Map of Yukon Showing Location of Study Area

been destroyed by fires at one time or another (Porsild, 1951). Stands greater than 170 years old can be considered late succession to climax forests. Stands 105 - 160 years old, which resulted from a burn about 170 years ago, were arbitrarily called mid-successional stands. Early successional stands are located in two parts of the study area. The northeast section burned about 60 years ago while in the far southwest corner a fire occurred approximately 110 years ago.

It is obvious that *Pinus contorta* quickly invades an area after a burn (Porsild, 1951), and remains in the stand for varying amounts of time depending on site conditions (the drier the site, the longer the species remains). The oldest stands appear to be dominated by *A. lasiocarpa* and in spruce-dominated, late successional stands, *Abies* contributes the only understory regeneration. It appears, therefore, that an *Abies* forest is the climax type and that succession takes at least 170 years to reach climax conditions depending upon site conditions. Figures 2 and 3 (Archibald and Russell, 1979) depict the study area in discrete age and height classes respectively and help explain its fire history.

Glacial influences on vegetation are reflected through soil parent materials. Porsild (1951) indicated that very poorly drained organic areas could be attributed to glacial boulder clay deposits. In many of the hygric sites such a situation does exist. However, some clayey soils can be

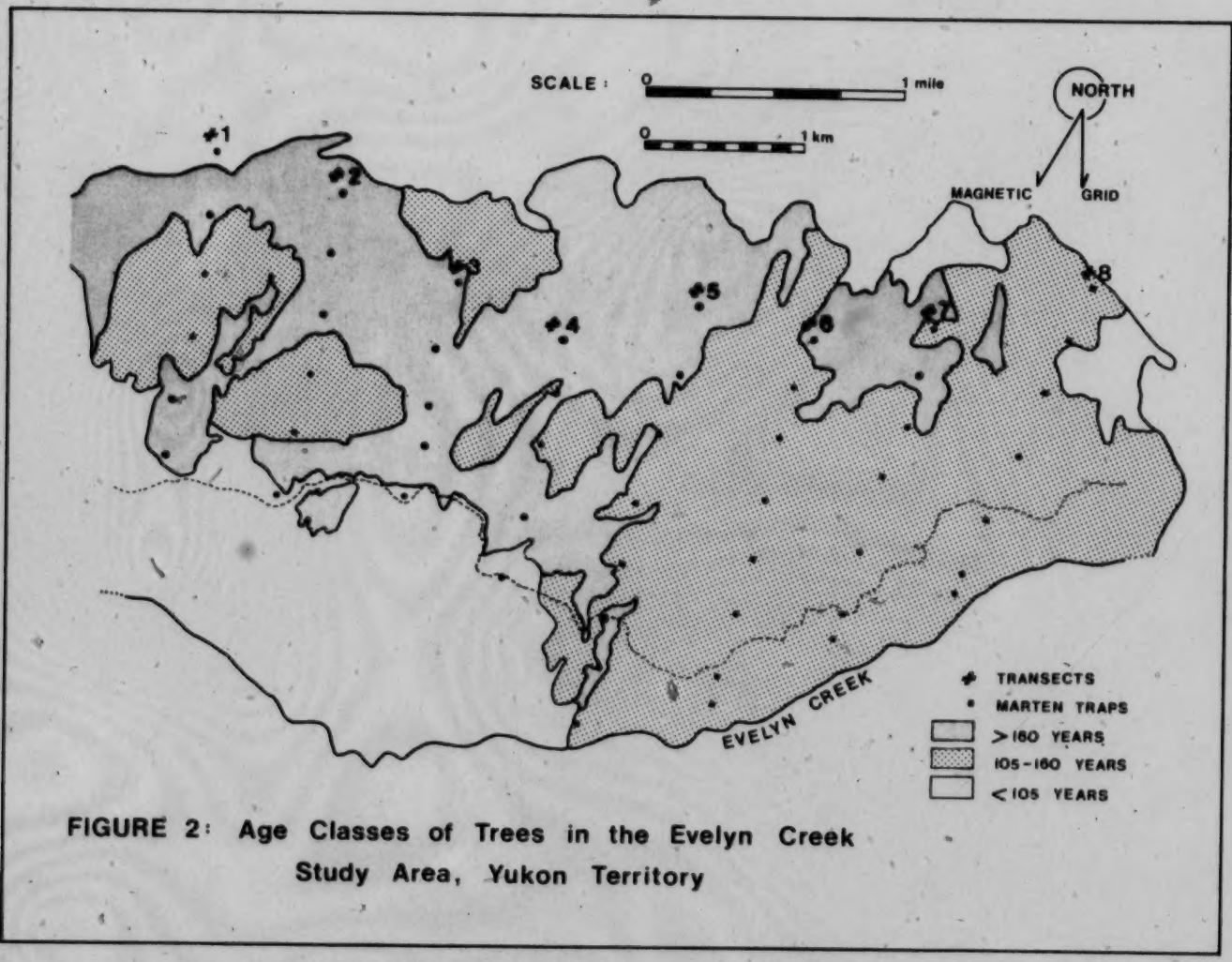


FIGURE 2: Age Classes of Trees in the Evelyn Creek Study Area, Yukon Territory

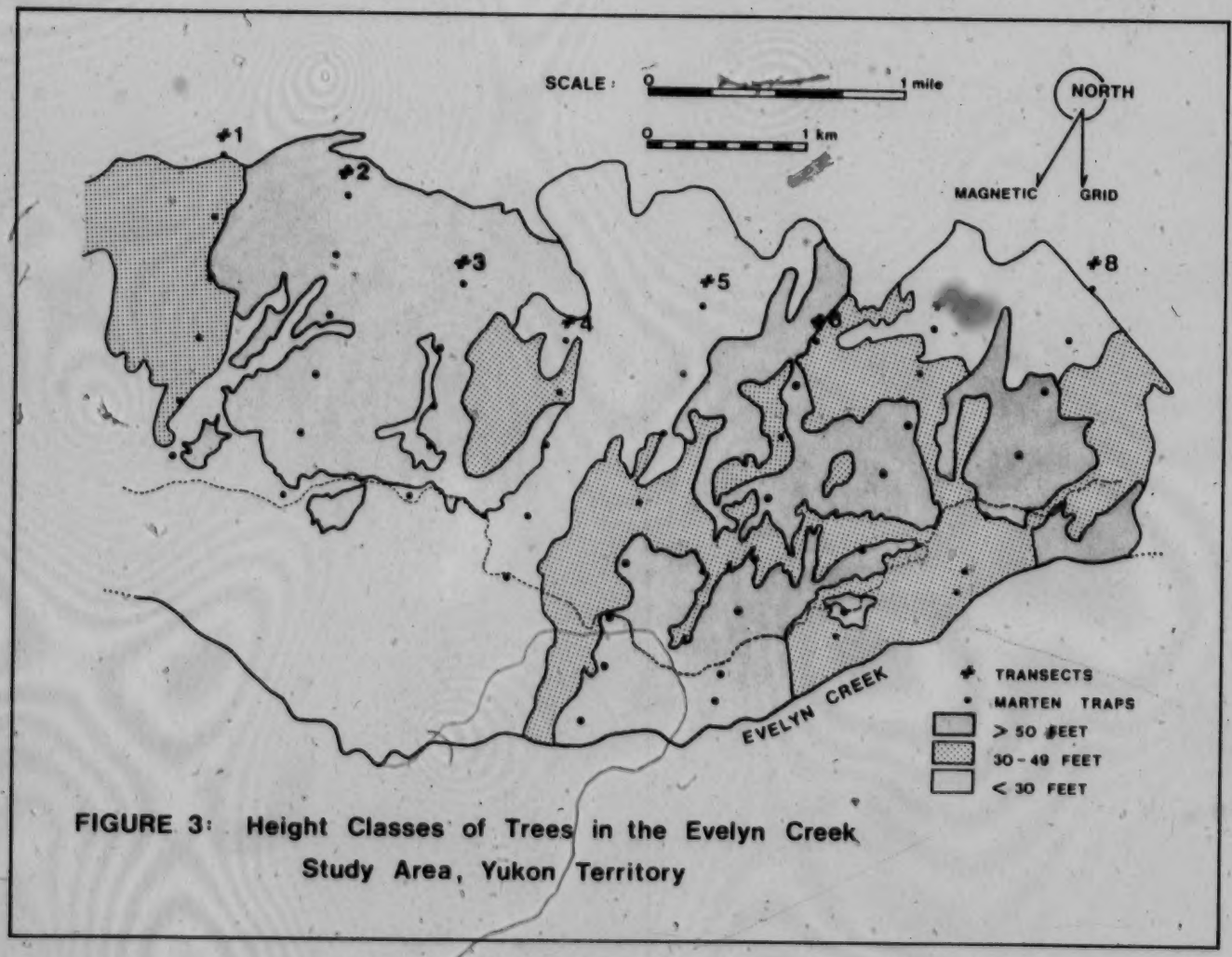


FIGURE 3: Height Classes of Trees in the Evelyn Creek Study Area, Yukon Territory

attributed to post-glacial decay of shale bedrocks (Porsild, 1951; Armson, 1977). This is true of higher elevation sites.

A sporadic white volcanic ash layer can be found throughout the area (Dawson, 1898; Lerbekmo *et al.*, 1975; Crampton, 1982). Porsild (1951) quotes other authors who suggested that this ash layer is approximately 1400 years old and was washed down from mountain slopes by wind and rain.

The climate in this area is continental with cold winters and moderately warm to warm summers. Snow cover usually lasts from October until May. Snow was much deeper and persisted longer at the higher elevations (Habitats II and V), than at the lower elevations at the base of the mountain (Habitats I, III and IV). The number of snow-free days each habitat experienced was similar in both years. Over the two summers of this study there was an average of 103.5 snow-free days (Table 1) and 79 frost-free days. These observations are consistent with those of Keele (1910) who concluded that 3 months of the year (25 May - 25 August) were practically frost-free. During the course of the field seasons (May - August, 1979 and May - September, 1980), there was an average of 60.5 days with rain and 64.5 days with at least some sunshine. The average maximum temperature over the two summers was 17.8°C, with a mean seasonal minimum of 3.6°C (Table 2).

METHODS

SMALL MAMMAL TRAPPING

1. Snap-Trapping in Habitats

Within each habitat type, snap-trapping of small mammals was conducted during the spring and fall of 1979 and 1980, and during the spring of 1981. Four lines, each consisting of 50 Museum Special snap traps baited with peanut butter, were established in each habitat type (Fig. 4). Care was taken to ensure that the entire trapline was placed in a single habitat type (Krebs and Wingate, 1976). Each line was run for 3 consecutive nights in spring (late May - early June) and again in fall (mid-September); thus, in each trapping period there were 600 trap-nights of effort in each habitat type. Trapping indices were not corrected for sprung traps or traps occupied by non-target species.

Although the calendar dates differ among years in the spring trapping, an attempt was made to trap at similar phenological dates. Trapping commenced when the amount of snow cover and air temperature were comparable among years (Table 3).

Museum Special traps are relatively efficient in the capture of murids (Martell, 1979), and several authors (ie. Inverson and Turner, 1973; Yang *et al.*, 1970; Stickel, 1946) are in agreement that snap-trapping is a reliable way of

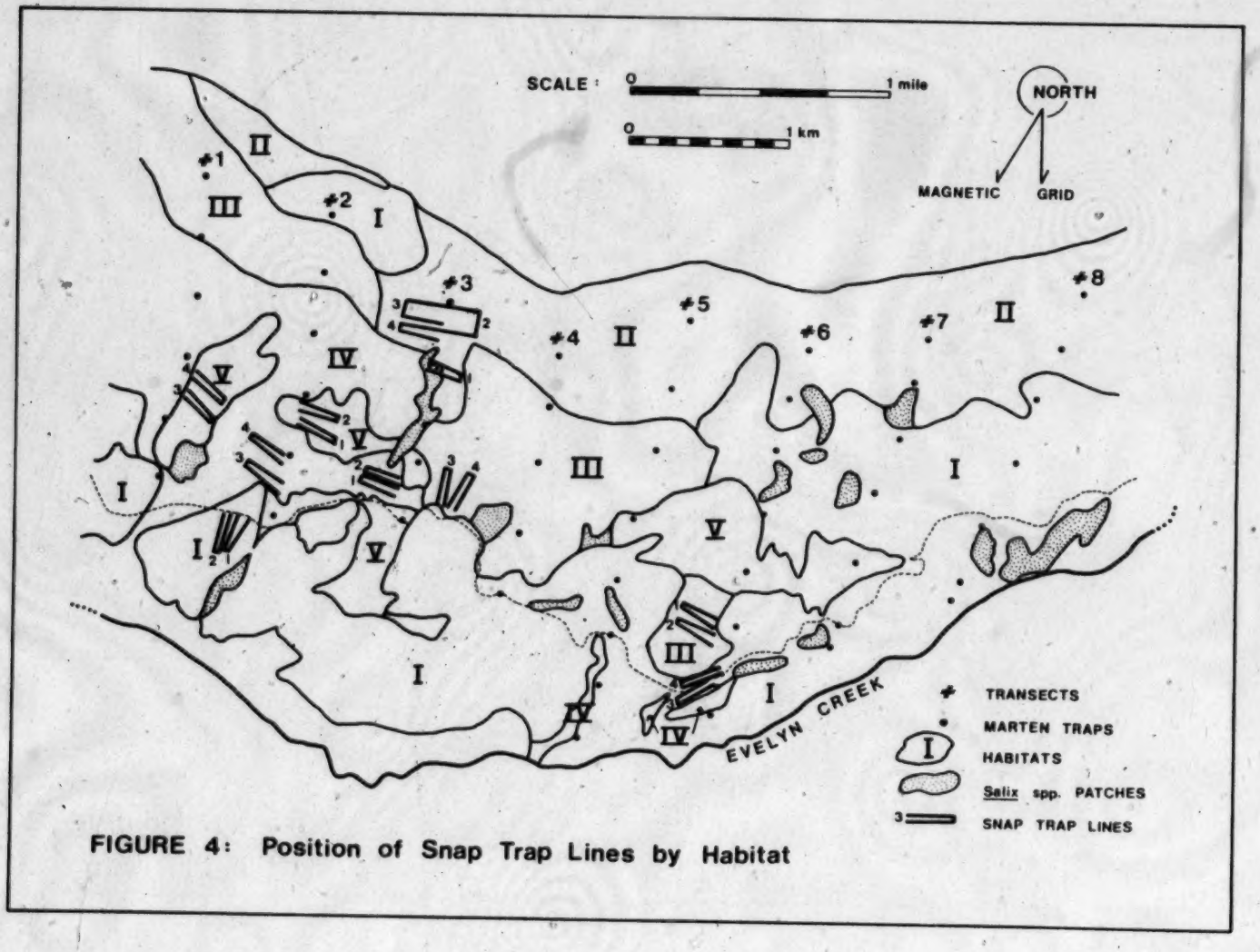


FIGURE 4: Position of Snap Trap Lines by Habitat

estimating relative numbers of small mammals. Pucek (1969) and Edwards (1952), however, indicated that it was difficult to estimate the population of Insectivora (*Sorex* and *Microsorex*) from snap-trap captures. Few shrews were taken in this study.

Trap stations were spaced at approximately 10 m intervals, as determined by pacing, and their positions were permanently marked in order to allow repeated sampling in the same locations. This trapping method may produce a bias (ie. trapper bias in the placement of traps), but since the bias was uniformly present (ie. one trapper), capture indices are considered to be indicative of relative population changes (Fuller *et al.*, 1975).

Autopsies were performed on all animals recovered dead from traps during the summer. Before opening, the carcasses were weighed to the nearest 0.1 g on an O'haus dial-o-gram balance and measured (total length, tail vertebrae, and hind foot) with a 30 cm Helix ruler. For males, length and width of the testis were recorded and occasional smears of seminiferous tubules and epididymis were made and examined on the spot for the presence of sperm. This procedure was usually followed for animals with testes of intermediate size. For females, visible embryos, placental scars and corpora lutea were recorded. When embryos were present, the crown-rump length of the embryo was measured to the nearest 0.1 cm and the weight of the reproductive tract was subtracted from the gross weight to yield a corrected body

weight.

2. Additional Snap-Trapping

In addition to the spring and fall snap-trapping of habitats, additional snap-trapping was done during the summer months (June - August) of 1979 and 1980. These traplines were located outside the study area, but in habitat types similar to those found in it. Each line consisted of 50 Museum Special snap traps, baited with peanut butter, and was positioned using the same techniques as those previously mentioned, but not permanently marked and not trapped repeatedly.

The purpose of this trapping effort was to furnish more information concerning the reproductive dynamics of *Clethrionomys rutilus* and to increase the sample size for data collected through autopsy. All small mammals collected in this aspect of the study were autopsied in the aforementioned manner.

Skulls were saved from all animals so positive identification could be made, if that was not possible in the field. After *C. rutilus* skulls had been cleaned in a dermestid beetle colony, their approximate age was determined from the development of the second upper molar (M^2) (Dickinson, 1976; Tupikova *et al.*, 1968).

3. Age Determination

Several methods of aging *Clethrionomys* spp. have been described (Mihok, 1980; Perrin, 1978; Lowe, 1971; Tupikova *et al.*, 1968; Viitala, 1971; Martell and Fuller, 1979). In this study, all autopsied *C. rutilus* were placed in one of four age classes according to the state of development of the second upper molar (M^2) as described by Martell and Fuller (1979). Skulls were examined under a Zeiss binocular dissecting microscope at x10. One maxilla (usually the right) was chipped away with a scalpel to expose the molar. The stage of development of the tooth was noted, and if roots were present, the root length, from the closure of the anterior groove along the anterior root, was measured by means of an ocular grid to the nearest 0.1 mm (Martell, 1975).

Four successive stages in development of the tooth were evident:

(i) anterior groove open,

(ii) anterior groove closed,

(iii) short roots (0.1 - 1.0 mm), and

(iv) long roots (>1.0 mm).

Overwintered animals were distinguished by the presence of roots greater than 1.0 mm in length. Young of the year animals were separated into three age classes depending upon the development of the molar. Age class I animals possessed a molar with the anterior groove open. Those individuals with the anterior groove closed were assigned to age class

II. Individuals in age class III had molar roots ≥0.1 mm and <1.0 mm. In terms of absolute age, if *C. rutilus* molars develop at about the same rate as those of *Clethrionomys gapperi*, then age class I animals were younger than about 30 days, age class II animals were between about 30 and 60 days, and age class III animals were older than 60 days (Mihok, 1980).

Live-trapped animals, for which skulls could not be obtained, were separated into weight classes. Those weighing more than 26.0 g were considered to be overwintered (OW) animals. Young of the year were arbitrarily placed in two categories:

(i) an older cohort, probably mainly age classes II and III, with weights of 18.1 - 26.0 g, or

(ii) a younger cohort, probably mainly age class I animals, weighing 18.0 g or less.

Age of embryos was established from weight and crown-rump length (Huggett and Widdas, 1951; Martell, personal communication). This information was used to back-date pregnancies to determine when conception probably took place.

4. Determination of Maturity

(i) *Males*

Males with scrotal testes, enlarged epididymides in which the tubules were visible to the naked eye (Nalbandov, 1976), and enlarged seminal vesicles were considered to be

reproductively active and therefore sexually mature. Presence of sperm in smears of testis or epididymis was also accepted as evidence of maturity. At the end of the breeding season individuals were found with testis flaccid and purplish in colour, lacking sperm in smears, but with accessory glands still enlarged. They were considered to be regressing, and therefore sexually mature.

Reproductively inactive males were those which had not attained sexual maturity at the time of capture. Immature individuals were characterized by abdominal testes, usually creamy white in colour and roughly 3 mm x 2 mm in size. The epididymides and seminal vesicles were small and epididymal tubules were not visible.

(ii) *Females*

Those females in reproductive condition were characterized by one or more of: an opaque or vascularized uterus, uterus with embryos or placental scars, corpora lutea in the ovary, much mammary tissue, moderate to large nipples (often surrounded by a hairless area), pubic symphysis open or parting.

In immature females the uterus was usually thread-like and transparent, only small follicles were present in the ovary, mammary tissue was virtually absent, nipples were not readily observed, and the pubic symphysis was closed.

5. Live-Trapping

In 1979, live-trapping was carried out on the four transects (numbers 2, 5, 6 and 7), that had the greatest variety of habitats. Transects varied in length from approximately 2000 to 3075 m and each passed through examples of at least three habitat types (Table 4). Several authors (Petticrew and Sadleir, 1970; Stickel, 1948a,b; Hansson, 1967) have suggested that index lines are an efficient method of sampling small mammal populations. The purpose of this trapping effort was to further determine habitat use by *C. rutilus*. By using live-capture data, in addition to the snap-trapping results, it was thought that if any habitat preference by *C. rutilus* existed, it could be demonstrated.

The total trapping effort in each habitat was approximately proportional to the area of each habitat present (Table 5). Longworth traps, with their large nest chamber, were used because it was important to provide bedding (terylene fiber) and food (sunflower seeds) for survival. Traps were placed at suitable locations (in runways, beside fallen logs or close to burrow openings) within 1 m of each permanent marker. Each trap was covered with moss, lichen, leaves or other forms of vegetation to protect captured animals from inclement weather and direct insolation. A trap interval of 29 m was required to cover

the total transect length with the number of traps (N=110) available.

Traps were supplied with fresh bait at the commencement of each trapping period, or rota, which began by opening the traps in the late afternoon or early evening of day 1. They were then checked, usually between 0700 and 1000, in the morning of days 2, 3 and 4, left set during the day, and revisited between 1900 and 2200 hours on days 2 and 3. In 1979, traps were picked up in the morning of the fourth day, rebaited, and reset on the next transect in the evening, where the same routine was repeated. In order to trap all 4 transects in 1979, a 13-day rota was needed. A week of snap-trapping outside the study area followed this and then the live-trapping was repeated. Therefore, each transect was live-trapped for a 3-day period every 3 weeks. Four rotas were conducted during the summer of 1979 (Table 6).

Because the capture rate on transects 2 and 7 during 1979 was low, effort was concentrated on transects 5 and 6 in 1980. Again, traps were placed at 29 m intervals and were left open for 3 nights. Enough extra traps were supplied so that both transects could be trapped at one time. Therefore, the rota began by opening the traps on both transects in the late afternoon or early evening of day 1 and they remained open until the rota ended on the morning of the fourth day (Table 6).

Six live-trapping sessions were conducted during the summer of 1980 in order to monitor the small mammal

populations on the two transects for a 3-day period every 2 weeks. There was a seventh and final rota in late September which consisted of 2 snap-traps placed at every live-trap location. Traps were checked every morning for 3 days and the animals collected in this trapping session were autopsied. The animals removed during this final rota provided information about reproductive history and age composition of the population, as well as being a check on the efficiency of live-traps (Table 7).

The trap mechanism was constantly checked for sensitivity, fresh bait was supplied after every capture and terylene was replaced as needed. Periodically, usually after every second rota, the traps were picked up, examined, brushed out, readjusted if required, and supplied with fresh bait and new bedding as needed. At least some old, used terylene was present in every trap and the traps were not cleaned in soapy water until the end of the summer, thus ensuring that the "mousy-smell" would remain in the trap to attract animals.

Captured animals were weighed and examined for external signs of sexual maturity: testes abdominal or scrotal if a male, vagina perforate or not-perforate, nipples visible or not-visible, and pubic symphysis open, parting or closed if a female. They were then released at the point of capture. On first capture, each animal was toe-clipped for individual identification.

VEGETATION SURVEY

To characterize the microtine rodent habitats over the study area an intensive vegetation survey was conducted. Five habitat types were identified by vegetation studies conducted by the Yukon Wildlife Branch in conjunction with a study of *Martes americana* which was underway at the time this project was undertaken. The purpose of this vegetation survey was to describe and characterize the habitats.

In each of the five habitat types, two 20 x 50 m (0.1 ha) macroplots were placed and the vegetation within them was analyzed. Macroplots were located in the same areas where the index snap-trap lines were situated. Since each trapline was completely within the habitat type it was to represent, the macroplots were also placed there in order to ensure that the vegetation surveyed was representative of that habitat type.

A uniform stand of the vegetation type was bisected by means of a 50-metre chain on an east-west line (baseline) where possible (north-south for vegetation plots 1-1 and 3-2). Information regarding slope angle, slope aspect, microrelief, drainage class and moisture regime was then recorded.

Within each macroplot, cover classes of the major growth-forms (ie. trees, shrubs, herbs and terrestrial bryoids) were recorded on a standard form (Appendix 1). Total cover class estimates were also made for the plant community as a whole, ie. irrespective of height. The plant

strata and substrata represented were arbitrarily named (eg. tall, medium and low shrub) and estimates in percent cover, as well as average stratum height and clarity of development (resolution: high - medium - low) were also recorded. At the 25 m mark on the baseline a soil pit was dug, from which the colour and thickness of each soil horizon were determined.

A 1 x 1 m collapsible frame was constructed in order to form a 1 m^2 microplot (quadrat) in which plant species could be assessed for height and cover class. Microplots were sequentially placed 5 m from the baseline at the 5, 15, 25, 35, and 45 m marks to the left, and at the 10, 20, 30, 40 and 50 m marks to the right of the baseline. These 10 quadrats per macroplot were used to assess the species composition and abundance of the understory shrubs and herbs. Plant nomenclature according to Hale (1969) and Hultén (1968).

The cover class of every plant species found in the 1 m^2 microplot and in the 0.1 ha macroplot was determined. This value consisted of a range that the actual percent cover was thought to be in (ie. 1 - 5%, 6 - 15%, etc.; see Appendix 1). Values of plant cover used in analyses involved the midpoints of these ranges of cover values.

A 5 cm Bitterlich wedge-prism was used to estimate stem cover (ie. basal area in ft^2/acre) of living and dead trees from survey points at the 5, 15, 25, 35 and 45 m marks on the baseline. The Bitterlich method allows for rapid and accurate analysis of stem cover by species in semicomplex

forest communities in which the undergrowth is primarily herbaceous (Mueller-Dombois and Ellenberg, 1974). When viewing through the prism, tree stems appear displaced to one side. Where the displacement is within the trunkline, the tree is counted; where the displacement is outside, the tree is ignored (Mueller-Dombois and Ellenberg, 1974). A borderline tree is counted as half-tree (Dilworth and Bell, 1967). Small-diameter trees are included in the count only if they are close to the observer, while large-diameter trees are included at greater distances away from the observer. The diameter at breast height (DBH) was recorded for the trees found to be "in" by the wedge-prism sightings. There is a bias in the tallies of tree DBH by the prism method, however, because a greater number of larger trees will be counted than smaller trees. However, this bias is consistent among habitats. In addition to the timber cruise, cover class estimates of each tree species in the macroplot by height class were also made. This information could give an indication of habitat quality, as usually fertile sites have high basal areas (La Roi, personal communication).

The mean cover class midpoint values of the plant species found in the habitat types were analysed statistically by a stepwise discriminant functions analysis. This was done in an attempt to delineate the habitat types using characteristic vegetation species. Species were not retained in the analysis unless the cover differed significantly among habitats at the $P = 0.05$ level. The

stepwise procedure initially selected the single best discriminating variable, or plant species. A second discriminating variable was selected as the variable best able to improve the value of the discrimination criterion in combination with the first, and so on until the remaining variables no longer contributed to further discrimination. When that point was reached, the stepwise procedure was halted and further analyses were performed using only the selected variables (Nie, *et al.*, 1975). This analysis was used in an attempt to see if habitats differed with regard to vegetation, and if so, which of the plant species best delineated the habitat types.

Each of the 340 live-trap sites was assigned to one of the five habitat types in 1979, during the months of July and August, when most vascular plants should have been flowering or fruiting. Plant species found within a 5 m radius of the trap location were identified and recorded on "Vegetation Observation Cards" designed by the Yukon Wildlife Branch (Appendix 2). Characteristic indicator plant species were then used to determine in which habitat category to place the trap site.

As a result of this information and similar vegetation analyses conducted by the Yukon Wildlife Branch (D. Russell, personal communication) a vegetation map was produced (Fig. 4).

RESULTS

VEGETATION ANALYSIS

Since a major aspect of this study deals with the habitat preferences of *Clethrionomys rutilus*, it was necessary to determine the various habitat types present within the study area. Forty-six species of shrubs, herbs, mosses and lichens were identified and included in a discriminant functions analysis (see Methods) in an attempt to classify the habitats on the basis of vegetation characteristics. Although only two cases (data from two vegetation plots per habitat) were included in the analysis, it was clear that the habitat types were different and the four indicator variables (*Equisetum arvense*, *Gramineae* spp., *Mitella nuda* and *Pleurozium schreberi*) correctly classified them 100% of the time (Table 8).

Other plant species also appeared to be characteristic of certain habitats and helped in their classification and identification. A summary of the important and diagnostic species comprising the habitats follows:

Habitat Type I, Pine Forest. This type is generally found on mesic or submesic sites on lower to middle slopes having well-drained sandy or silty sand soils (Table 9). Generally the habitat is located on the lower slopes or flats in the north-east section of the study area. The

overstory consists primarily of *Pinus contorta* although *Abies lasiocarpa* and occasionally *Picea glauca* do occur. This habitat is easily distinguished from the rest as it is the only one dominated by an overstory of *P. contorta* (range of cover class midpoints 10.0 - 20.0%, Table 10). Two distinctly different areas of type I can be found. In the north-east section of the study area, this type dominates a 70-year-old burn whereas in the far western portion it occurs as a 180-year-old stand (Don Russell, pers. comm.).

The shrub layer is moderately well-developed with patchy *Abies lasiocarpa* regeneration (although none were observed in the microplots), some *Pinus contorta* regeneration, *Empetrum nigrum* (which attained its highest mean cover of 22% here), *Ledum palustre*, *Vaccinium uliginosum* and *Vaccinium vitis-idaea* (again the most of any habitat at 4% cover, Table 11) normally occurring. Shrubs of low to medium height (9 - 40 cm) made up the majority of the shrub cover with 29%, whereas taller shrubs (mean height 2 m) contributed 2% to the total shrub cover.

The herb layer is poorly developed with low species richness (8 species) and abundance (3% cover). *Cornus canadensis*, *Lupinus arcticus*, *Lycopodium annotinum* and *L. complanatum* are the main herb species present. *Epilobium angustifolium* is present only in this habitat in the microplots, but only in trace amounts (0.03% mean cover, Table 12).

A well-developed terrestrial lichen layer, second only to Habitat II in abundance, is present within this habitat type. Lichen species diversity is greatest (9) in this habitat (Table 13). *Cladonia* sp., *Cladina mitis*, *Cladina rangiferina* and *Peltigera aphthosa* can usually be found. *Cladina stellaris* is present only in this habitat. Mosses however, are very poorly developed with the least abundance (7% mean cover) found in any habitat. Mesophytic mosses are the main representatives, contributing 5.7% mean cover to the total moss abundance (Table 13).

Habitat Type II, Fir Forest. This type normally occurs on mesic middle and upper slopes. Soils on these sites tend to be well- to moderately well-drained, shallow, and derived from glacially-deposited sands and clays weathered *in situ* (Don Russell, pers. comm., Table 9).

The tree layer in these higher elevation forests tends to be thin and consists almost exclusively of *Abies lasiocarpa*. Some *Pinus contorta* and *Picea glauca* (3% combined cover out of a total tree cover of 41%, Table 10) can occasionally be found in the overstory, but seldom if ever in the understory. The shrub layer has the lowest species diversity (9) and the lowest mean cover (11%) of any habitat. Seedling-sized *A. lasiocarpa* (5%) and *Empetrum nigrum* (4%) dominate the understory of this habitat (Table 11). The remaining 7 species, except *Ribes triste*, have the lowest estimated abundance of any habitat type. Although its mean cover was very low (0.05%), *R. triste* was present only

in this habitat, and therefore is a good habitat indicator species.

The herb layer, in contrast, has a high species diversity (17), however not a very large abundance (4% mean cover, Table 12). *Cornus canadensis*, *Equisetum arvense*, *Lupinus arcticus*, *Pyrola* sp. and *Moneses uniflora* (the latter absent from all 1 m² microplots) normally occur in this type.

This habitat type has the most extensive lichen layer (mean cover = 26%) of any habitat. *Cladina mitis* is at its greatest abundance here (mean cover = 12%), and *Cladonia* sp., *Peltigera aphthosa* and *Nephroma arcticum* are also common here. The feather moss, *Pleurozium schreberi*, occurs in high abundance throughout most of these stands, probably as a result of colder temperatures and higher relative humidity.

Habitat Type III, Fir-White Spruce-Pine Forest. This type is found in mesic to subhygric sites on middle to lower slopes (Table 9). Soils, primarily of clay and sandy parent material, are generally imperfectly to poorly drained, and in many sandy soils, buried clay horizons prevent rapid drainage. Both sites where type III was analyzed contained permafrost layers with low ice content.

As with Habitat Type I, two distinctly different areas exist with regard to the overstory. Vegetation plot 3-1 consisted of a *P. glauca* dominated stand 105 - 160 years old, with *Abies lasiocarpa* regeneration in the understory,

whereas plot 3-2 was in a stand dominated by both immature and mature *A. lasiocarpa* 175 years old or older.

The shrub layer is moderately well-developed with 11 species, and a cover value of 17%. *Abies lasiocarpa* layers and seedlings dominate the stratum (9%, Table 11) and achieve their greatest abundance in this habitat. Other important shrubs include *Empetrum nigrum* and *Vaccinium vitis-idaea*, which make up 6% of the 9% mean cover. *Alnus crispa* was observed in this habitat, but it did not show up in any of the microplots.

The herb layer is poorly developed with only 10 species represented. However, its mean cover of 8% is the third highest (Table 12). Commonly found species in this type are *Cornus canadensis*, *Petasites* sp., *Pyrola* sp., *Rubus chamaemorus*, *Lycopodium annotinum* and *Moneses uniflora* (even though none were observed in the microplots). *Cornus canadensis*, *Pyrola* sp. and *L. annotinum* reach their greatest abundance in this habitat.

The lichen layer is moderately well-developed with 6 species present and a mean cover of 8% (Table 13). *Peltigera aphthosa*, *Nephroma arcticum* and *Cladina mitis* are the most represented species, with a combined mean cover of 7%. The moss layer has the highest mean cover of 83% in this habitat. *Pleurozium schreberi* normally forms dense carpets in these sites and mesophytic mosses are at their greatest abundance here. Habitat Type III is one of two in which *Sphagnum* spp. are present (10% mean cover).

Habitat Type IV, White Spruce Forest. This type is located on moderately well-drained mesic lower slopes in the study area. Soils are generally sandy to sandy-clay with a comparatively high loam content (Table 9) and some permafrost present. The organic horizon is better developed in this habitat type than in the others, with a well-decomposed layer of humus averaging 19 cm thick.

Picea glauca comprises virtually the entire overstory with a mean cover of 38% (Table 10); the remaining 3% is contributed by an *Abies lasiocarpa* understory. As *Pinus contorta* is present in every other habitat, in varying amounts, a distinguishing characteristic of this habitat type is the absence of *P. contorta* in both over- and understory.

The shrub layer of this habitat is very well-developed with a high species diversity (12) and the highest mean cover of any habitat at 41% (Table 11). *Abies lasiocarpa, Picea glauca, Alnus crispa, Betula glandulosa* and *Salix* spp. form the tall shrub component (mean height = 1.9 m) with a combined mean cover of 14%. *Arctostaphylos rubra, Empetrum nigrum, Ledum palustre, Potentilla fruticosa, Vaccinium uliginosum* and *V. vitis-idaea* dominate the low shrub component (mean height = 24 cm) with a combined mean cover of 26%. *Picea glauca* seedlings, *A. crispa, A. rubra, B. glandulosa* and *P. fruticosa* all achieve their greatest abundance in this habitat and therefore could be considered diagnostic species.

In addition to having a very high shrub species diversity, Habitat Type IV boasts the highest diversity of herbs at 18 species. The mean cover is moderate at 8%, second only to Habitat V. Among the common species occurring in this habitat type are *Cornus canadensis*, *Geocaulon lividum*, *Linnaea borealis*, *Mertensia paniculata*, *Mitella nuda*, *Pedicularis labradorica* and *Rubus arcticus* with a combined mean cover of 6% (Table 12). With the exception of *C. canadensis*, all reached their greatest cover in this habitat. *Senecio triangularis* was present in this habitat and no others; however, it was observed only in the macroplot and not in any of the microplots.

Lichens are very poorly represented here with *Cladina mitis* and *Nephroma arcticum* the only species present in more than trace amounts (Table 13). *Pleurozium schreberi* is at its greatest cover (71%) in Habitat Type IV where it normally forms an almost continuous carpet in these moist sites.

Habitat Type V, Spruce-Fir Woodland. This type occurs on the wettest sites of the study area. Moisture conditions range from mesic to hygric on middle slopes. Permanently frozen soil is common, resulting in sparse tree growth and, normally, a predominance of shrubs and herbs.

The tree layer consists generally of *Picea glauca* and *P. mariana*. However, due to uncertainty in the separation of these two species, they were unfortunately combined under the common heading of "spruce". The tree layer is normally

sparse, due in part to the harsh growing conditions in this area. *Abies lasiocarpa* is also present but mainly in the understory with a mean cover of 10% (Table 10).

The shrub layer of this habitat is well-developed in regard to species diversity (12) and possesses a moderate mean cover of 25%. Moisture-loving *Salix* spp. has its greatest cover in this type and as such is a good diagnostic genus. *Vaccinium uliginosum, V. vitis-idaea, Arctostaphylos rubra* and *Ledum palustre* are well represented here; 12% of the shrub cover is accounted for by these four species (Table 11).

The herb layer is moderately rich in species (16) and possesses the highest mean cover (10%) of any habitat. *Carex* sp. is particularly diagnostic of this type as it reaches its greatest mean cover here at 10% (Table 12). Other species that reach their maximum mean percent cover here are: *Equisetum arvense, E. silvaticum, Gramineae* spp., *Petasites* sp., and *Rubus chamaemorus* with a combined mean cover of 6%. *Linnaea borealis* and *Rubus arcticus* are also common species.

The lichen layer is species poor (5 species) and has the lowest mean cover (2%) of the five habitats. *Cladina mitis, C. rangiferina* and *Peltigera aphthosa* are the only species of any significance. Mosses are relatively abundant in this type with *Pleurozium schreberi*, mesophytic mosses and *Sphagnum* spp. well represented throughout for a combined mean cover value of 62%. *Sphagnum* spp. reaches its greatest

cover in the macroplots and is therefore a good diagnostic genus (Table 13).

SPECIES DIVERSITY

The diversity of a community as measured by the Shannon-Wiener function (H) depends on two things: the number of species and the evenness with which the individuals are apportioned among those species (Pielou, 1975). A greater number of species increases species diversity, and a more even or equitable distribution among species will also increase species diversity (Krebs, 1978). The diversity value is a measure of the amount of uncertainty in predicting the species of the next individual collected, so that the larger the value (H), the greater the uncertainty. According to Krebs (1978), this approach is preferred by some because it is independent of any hypothetical distribution such as the log-normal. The Shannon-Wiener function was used as a satisfactory measure of diversity following Huhta (1979).

The diversity of the small mammals captured in both spring (Table 14) and fall (Table 15) trapping periods was calculated for each habitat and each year using the basic Shannon-Wiener function (Krebs, 1978):

$$H = -\Sigma Pi \log_2 Pi$$

In this formulation, H=information content of sample in bits/individual which is the index of species diversity; and *Pi* = the proportion of the *i*th species in the sample.

Equitability or evenness of allotment of individuals among the species (J) was calculated as:

$$J = H/Hmax$$

where J=equitability (range 0-1), *Hmax* = maximum species diversity=Log_2 S; S=number of species (Krebs, 1978).

The diversity and evenness of the small mammals captured in the spring (Table 14) showed no pattern. To make seasonal comparisons total captures for spring trapping (Table 16) and fall trapping (Table 17) were combined across years. There was a tendency for both diversity and evenness to decrease from the spring to fall in all habitats but I, due undoubtedly to the increase in captures of one species (*C. rutilus*) in the fall censusing periods. Habitat V had the greatest diversity in both seasons (H=1.65 in spring and H=1.31 in fall). In addition, Habitat V possessed the greatest evenness (J=0.71 in spring and J=0.47 in fall). Habitat II, however, had a relatively low diversity in both seasons due, probably, to the large number of individuals captured of a (relatively) small number of species. The diversity and evenness in Habitat I went from low in the spring to moderate in the fall largely due to the appearance of shrews in the fall sample. The evenness across all

habitats was generally low because of the dominance of *C. rutilus* in the samples.

The diversities of small mammals were then compared by means of a measure termed DIVdif (Dd) (Järvinen and Sammalisto, 1973). Dd is defined as:

$$Dd = H_{i,j} - (H_i + H_j)/2$$

That is, as the difference between the common diversity of 2 habitats, ($H_{i,j}$) and the mean diversity of the same two habitats [$(H_i + H_j)/2$] (Järvinen and Väisänen, 1973). Consequently, Dd is that part of the total diversity that is due to pooling the two areas, that is, due to differences between the areas. It provides a measure of the difference in species composition between two areas.

This value was then incorporated into a modification of the index Dd. The new index, relative DIVdif (rD) has a range from 0 to 100 (%) and is defined by Järvinen and Väisänen (1976) as:

$$rD = 100[\exp(Dd) - 1].$$

That is, "100 times the ratio of 'equally common species' in the combined area to the geometric mean of the numbers of 'equally common species' in the two areas, minus 100. This transformation of DIVdif avoids the logarithmic nature of DIVdif." In other words, if exponents are calculated on the

same base as the logarithms originally used to calculate H, rD is independent of the log system used (Järvinen and Väisänen, 1976).

Values of rD are presented for both spring (Table 18) and fall (Table 19) capture data. High rD values mean low similarity; thus, the spring data (Table 20) show that Habitats I and V were most different with respect to small mammal diversity, with 28.8% of the total rD between them. Habitats III and IV were most similar, with only a 2.8% difference in relative small mammal diversity (rD) between them. In the fall data (Table 20) Habitats I and V were again most dissimilar with respect to small mammal diversity, with 30.9% of the total rD between them. Habitats I and II and II and IV had rD's of zero and Habitats II and III (rD = 0.89) and I and III (rD = 1.25) had very low rD's indicating that they had either no or very little difference in relative small mammal diversity between them. The two sets of habitat ranks (spring and fall) are independent of one another (Rs = 0.46, Z = 1.39; Spearman's Rank Correlation Coefficient) which means that rD changed seasonally.

Like H and J, Dd and rD were consistently lower in fall than spring in spite of a) more species and b) larger catches. This is a result of the dominance of a single species of microtine, *C. rutilus* (80.4% of the catch in spring, 87.4% in fall).

RELATIVE ABUNDANCE OF *Clethrionomys rutilus*

Clethrionomys rutilus, which inhabited all habitat types and constituted 82.3% of the total catch, was clearly the dominant species (Figures 5 and 6). No other species was taken in all habitats, and none approached *C. rutilus* in abundance. With great consistency, Habitats II and III yielded the greatest numbers of *C. rutilus* (Appendix 3) whereas the fewest individuals were removed from Habitats I and IV.

The numbers of *C. rutilus* captured in different habitats were compared by means of One-way Analyses of Variance (ANOVA). The spring data revealed no significant differences in the number captured among habitats, either for the sexes combined ($F_{(4,15)} = 1.44$) or for each sex separately (male $F_{(4,15)} = 1.31$; female $F_{(4,15)} = 1.52$). The fall trapping, however, revealed that numbers of *C. rutilus* captured differed significantly according to habitat type (sexes combined: $F_{(4,35)} = 9.09$, $P<0.001$). Males and females considered separately, also showed significant differences (males: $F_{(4,35)} = 6.95$, $P<0.001$; females: $F_{(4,35)} = 5.73$, $P<0.005$) among habitats. Student-Newman-Keuls (SNK) tests were performed upon these data to determine where the differences occurred. For sexes combined (Table 21) and for males (Table 22) tested separately, captures in Habitats II and III differed significantly from those of Habitats I, IV and V. When the females are considered alone, Habitats II and III are again significantly different from Habitats I

Figure 5. Catch per 100 trap-nights of small mammals in the five habitat types, 1979. Sexes combined. (N) = sample size. Abbreviations for small mammals:

C.r. = *Clethrionomys rutilus*
L.s. = *Lemmus sibricus*
M.p. = *Microtus pennsylvanicus*
P.i. = *Phenacomys intermedius*
S.b. = *Synaptomys borealis*
S.c. = *Sorex cinereus*
S.o. = *Sorex obscurus*

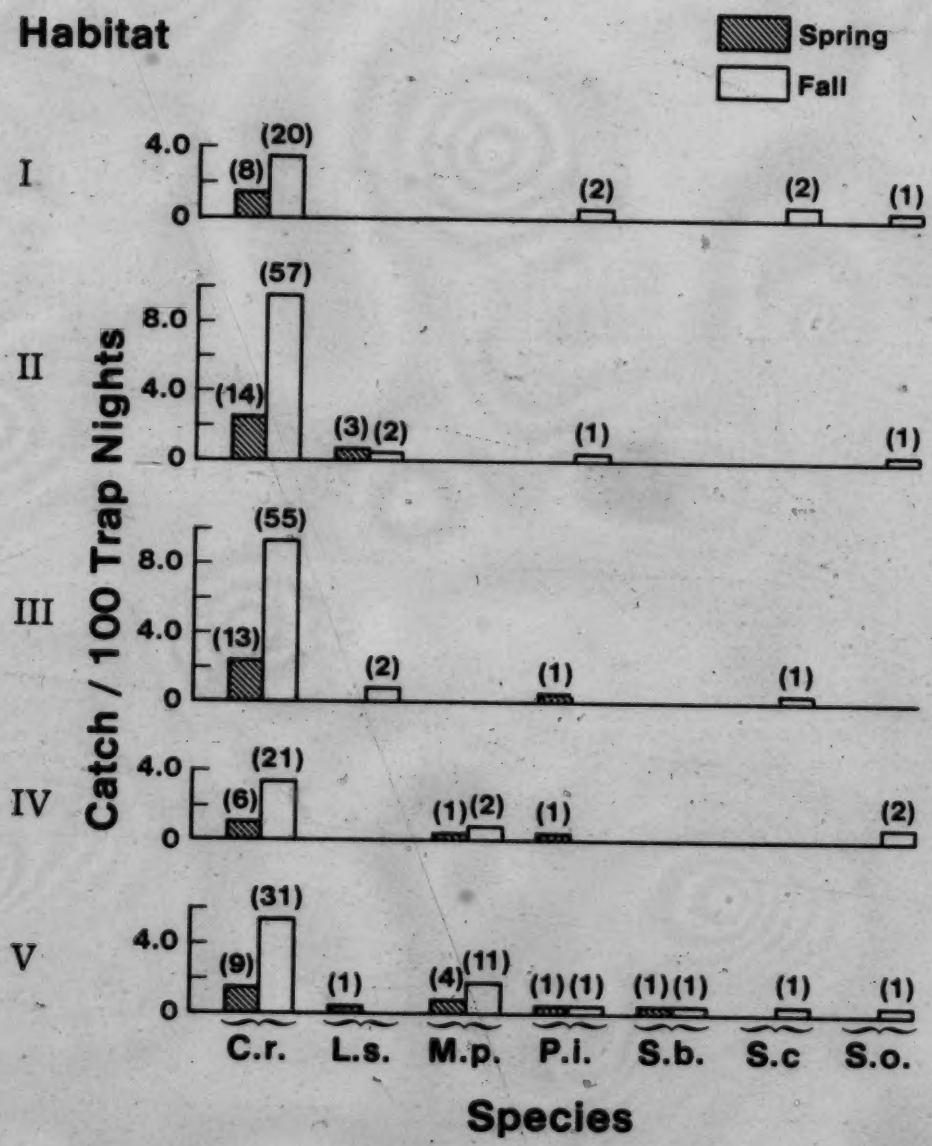
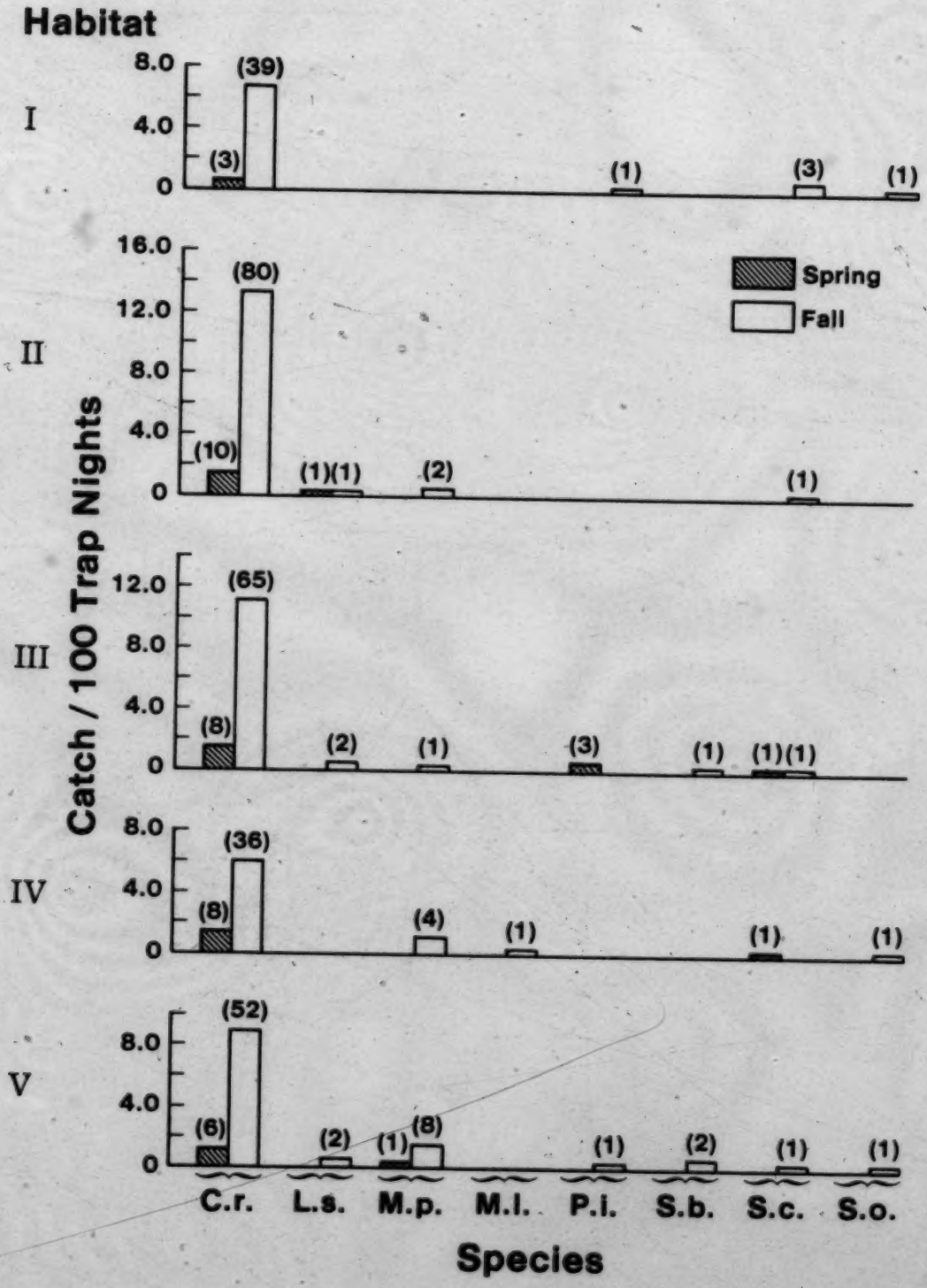

Habitat
Spring
Fall
I
II
III
IV
V
4.0
8.0
0
(8)
(20)
(2)
(2)
(1)
(14)
(57)
(3)
(2)
(1)
(1)
(13)
(55)
(2)
(1)
(1)
(6)
(21)
(1)
(2)
(1)
(2)
(9)
(31)
(1)
(4)
(11)
(1)
(1)
(1)
(1)
(1)
(1)
Catch / 100 Trap Nights
C.r.
L.s.
M.p.
P.i.
S.b.
S.c
S.o.
Species

Figure 6. Catch per 100 trap-nights of small mammals in the five habitat types, 1980. Sexes combined. (N) = sample size. Abbreviations for small mammals:

Same as Figure 5 plus:

M.l. = *Microtus longicaudus*


Habitat
I
II
III
IV
V
8.0
4.0
0
16.0
12.0
8.0
4.0
0
12.0
8.0
4.0
0
8.0
4.0
0
8.0
4.0
0
(39)
(3)
(1)
(3)
(1)
(80)
(10)
(1)(1)
(2)
(1)
(65)
(8)
(2)
(1)
(3)
(1)
(1)(1)
(36)
(8)
(4)
(1)
(1)
(1)
(52)
(6)
(2)
(1)
(8)
(1)
(2)
(1)
(1)
Spring
Fall
Catch / 100 Trap Nights
C.r.
L.s.
M.p.
M.l.
P.l.
S.b.
S.c.
S.o.
Species

and IV, but not from Habitat V (Table 23).

Since the fall sample is composed of animals of different ages, each age class was separately analyzed by 1-way ANOVA to determine whether the mean number captured differed significantly according to habitat type. The sample of overwintered (OW) animals was small, and perhaps as a result, revealed no significant differences ($F_{(4,35)}$ = 2.55). The sample size was also quite small for age class III; however, a significant difference at the $P<0.05$ level was noted ($F_{(4,35)} = 3.52$). The subsequent SNK test (Table 21) revealed that Habitat III was significantly different from Habitat I with respect to mean trapline captures, but was not different from Habitats II, IV, and V.

For age class II, significant differences among habitats appeared for sexes combined ($F_{(4,35)} = 5.66$, $0.005<P<0.001$), and for each sex separately (male: $F_{(4,35)}$ = 3.89, $P<0.025$; female: $F_{(4,35)} = 4.07$, $P<0.01$). Means were then compared by way of SNK tests which revealed that with the sexes combined there were two homogeneous groups (Table 21). Mean captures in Habitats II and III were significantly greater than those in Habitats I and IV. For males alone, Habitats II and III had significantly more captures than Habitat IV, but not Habitats I or V (Table 22). With regard to females alone, Habitat II differed significantly from Habitats I and IV, but not from Habitats III and V (Table 23).

When age classes II and III were combined, significant differences among habitats appeared for sexes combined ($F_{(4,35)} = 5.56$, $0.005<P<0.001$), and for each sex separately (male: $F_{(4,35)} = 4.30$, $P<0.01$; female: $F_{(4,35)} = 3.87$, $P<0.025$). When the means were compared by way of SNK tests, Habitats II and III were significantly different from Habitats I and IV, but not from Habitat V with the sexes combined (Table 21) and for males alone (Table 22). For females alone, (Table 23) mean captures in Habitat II were significantly greater than those in Habitats I and IV.

For age class I, significant differences among habitats appeared for sexes combined ($F_{(4,35)} = 3.31$, $P<0.025$) and for females alone ($F_{(4,35)} = 2.84$, $P<0.05$) but not for males alone ($F_{(4,35)} = 1.94$).

The fall trapline captures were then subjected to a 2-way ANOVA (Appendix 4) which showed a highly significant difference between habitats in numbers of small mammals captured ($P<0.001$), but no significant difference between sexes. An SNK test (Table 24) conducted on these data revealed that for both sexes the greatest numbers were captured in Habitats II and III, with Habitats I and IV yielding the smallest number of *C. rutilus* in the fall and Habitat V intermediate.

SEX RATIOS

Sex ratios were examined by means of the G-statistic, corrected for continuity (Sokal and Rohlf, 1981) to check for differences among habitats and years. In those animals captured in the spring, there were no significant deviations from 1:1 in any of the three years when captures from all habitats were combined (Appendix 5). The only habitat in which the sex ratio deviated from 1:1 was Habitat V in 1979, where significantly more males (N=9) than females (N=0) were caught ($G = 8.62$, 1 d.f., $P<0.005$).

Although the proportion of males varied among habitats and over the years, the pooled values were constant among the three spring samples: 0.59 in 1979, 0.57 in 1980 and 0.58 in 1981 (Appendix 6).

Owing to the small size of the sample (N=15) caught in summer, 1979, no analyses could be done. In the 1980 summer-caught sample there were no significant deviations from the 1:1 sex ratio in any habitat or age class (Appendix 7, G-tests for Replicated Goodness of Fit). The proportion of summer-caught males in the overwintered category (56%) was not significantly different from the proportion captured in the spring (57%) or fall (52%) of the same year, which indicates that there was no differential mortality between the sexes, at least in 1980.

Age class II and age class III *C. rutilus* deviated significantly from the 1:1 sex ratio (Table 25) in both the 1979 and 1980 fall capture data. Significantly more males

than females of age class II were caught in 1980 (Gp = 11.03, P<0.005), but not in 1979 (Gp = 2.89, N.S.). This situation was reversed in age class III in which more females were caught in 1979 (Gp = 7.72, P<0.01) but not in 1980 (Gp = 3.62, N.S.).

The reason for this reversal in sex ratios is probably a sex-related difference in rate of development of the second upper molar (M^2) (Dickinson, 1976). Dickinson (1976) suggested that female *C. rutilus* may have a more rapid rate of M^2 growth than males before closure of the anterior groove, or the M^2 closure may take place at an earlier age in males than females, or the males may have the same rate of growth as the females, but a greater rate of attrition. To check for equality of sexes in all early-born young, age classes II and III were combined. In 1979 there was no departure from 1:1, but in 1980, there was still a marginally significant excess of males (Gp = 3.88, P=0.05).

Analysis of sex ratios across habitats revealed that only Habitat III showed a significant excess of males (of age class II) in 1979 (G = 6.40, 1 d.f., P<0.025) (Table 25).

Although not significant (G = 0.23 in 1979-80; G = 0.33 in 1980-81), the proportion of males in spring was higher than the proportion of males of all age classes in September of the preceding year. Those animals born late in the summer (age class I) form the bulk of the winter population (Fuller, 1977b). When the proportion of OW males caught in

the spring was compared with the proportion of age class I males of the previous fall, no significant differences were noted (G = 0.05 for 1979-80; G = 2.45 for 1980-81). Similarly, when age classes II and III were combined, the proportion of males did not change from fall to spring (G = 0.49 for 1979-80; G = 0.04 for 1980-81). This implies that regardless of age class the proportion of males in the population remained relatively constant from fall to spring. The real significance of these findings, however, is that there was no differential mortality between the sexes among the seasons. Mature males did not undergo greater losses, as was observed in *Clethrionomys rufocanus* by Kalela (1971).

There was a tendency for the proportion of males in Habitat II to increase from the fall to the spring of the following year. No other habitat showed this trend over the two winters; however, the crude proportion of males increased in all habitats except Habitat V during the winter of 1980-81.

Sex ratios were then determined for those *C. rutilus* removed from the live-trap lines in 1980 and similar results were observed (Appendix 8). Age classes I and IV (OW) showed no significant deviation from the expected 1:1 sex ratio, but age classes II and III did. Age class II showed a significant bias in favour of males (Gp = 8.64, 1 d.f., $P<0.005$), whereas females were more numerous in age class III (Gp = 12.09, 1 d.f., $P<0.005$). When both age classes were combined to check for equality of sexes in all

early-born young, no significant deviation was observed (G = 0.99, 1 d.f., N.S.).

The proportion of males captured in the fall of 1980 did not differ significantly between areas snap-trapped and those live-trap areas censused with snap-traps, in any age class or habitat. Since no significant differences were noted between the two kinds of trapping in 1980, the results were pooled and compared with the proportion of males captured in 1979. Again, no significant differences were noted in any age class or among habitats.

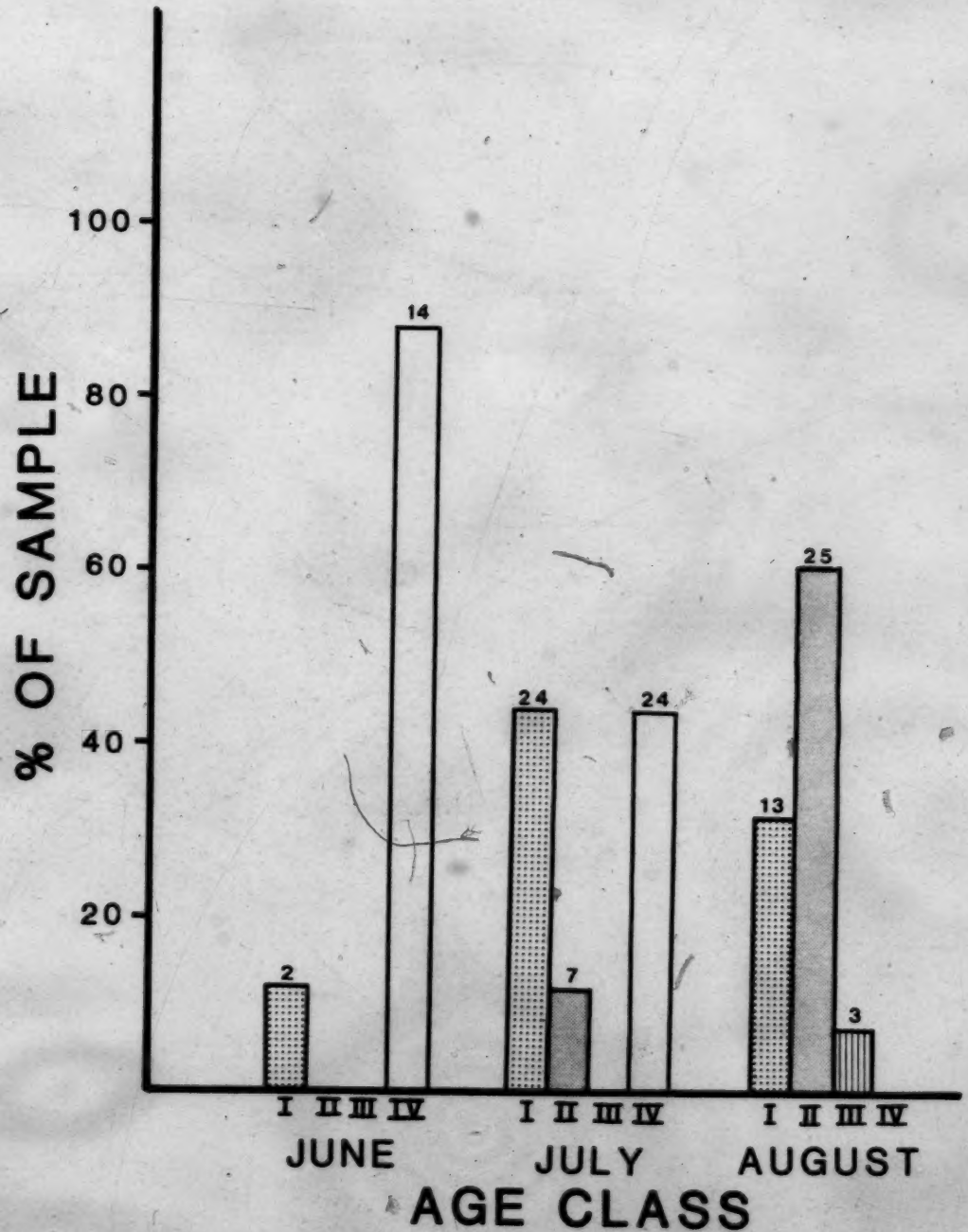
AGE STRUCTURE

To determine if the proportion of age classes of *C. rutilus* differed among the habitats, ages of all animals were determined and analyses were performed upon these data.

As would be expected, only overwintered (OW) animals were captured in the spring trapping periods (with one exception - a young male captured in Habitat IV in 1979, at the end of the spring trapping session), and young of the year individuals dominated the fall captures.

Certain trends concerning the age structure of *C. rutilus* were revealed when the supplementary trapline data were analyzed. Overwintered animals declined through the summer from their peak in the spring (Fig. 7). The majority (88%) of captures in June consisted of OW animals; however, none were captured in August of either 1979 or 1980. No age

Figure 7. Proportion of age classes of *C. rutilus* captured on the supplemental traplines. Years and sexes combined.


% OF SAMPLE
100
80
60
40
20
2
14
24
7
24
13
25
3
I II III IV
I II III IV
I II III IV
JUNE
JULY
AUGUST
AGE CLASS

class I individuals were captured in May and two (12%) were captured in June. The peak (44%) abundance of individuals of age class I was in July, with August seeing a slight decline to 32%. Fewer animals were breeding in August, and consequently fewer age class I individuals were present in the population. Age class II animals first appeared in July but in relatively low abundance (13%) because members of this age group were members of first seasonal litters. The numbers of individuals of this age class peaked in August (61%) mainly because age class I animals from July had attained age class II in August. Age class III *C. rutilus* were rare and present only in August (7%) and September (9%).

When the total numbers of *C. rutilus* (sexes combined) over all habitats in the falls of 1979 and 1980 are compared by age class, some differences emerge. The proportion of age class I animals decreased significantly (55% to 34%; $P = 9.4 \times 10^{-7}$, Fisher's Exact Test) from 1979 to 1980 (Table 26), while the proportion of age class II individuals increased significantly (32% to 48%; $P = 9.8 \times 10^{-5}$). No difference in proportion ($P = 0.23$) was noted in age class III animals between years (9% to 10%); however, when age classes II and III were combined the proportion increased significantly (42% to 58%; $P = 0.0001$) from 1979 to 1980. Finally, age class IV, the overwintered individuals, showed a significant increase in proportion ($P = 0.05$) over the two years. Taken together, these findings suggest that the mean age was older

in 1980 than in 1979. In the case of OW animals, survival may have been better in 1980 than in 1979, and in the case of young of the year, the older average age may have resulted from the earlier onset of breeding.

To see if habitat had any effect on age structure, fall capture data were compared among habitats by G-tests of independence. The proportion of age class I animals was significantly greater in 1979 in Habitats II ($G = 18.21$, $P<0.005$), III ($G = 4.46$, $P<0.05$) and V ($G = 4.24$, $P<0.05$) than in 1980 (Table 27). The proportion of age class I animals was also greater in Habitats I and IV in 1979, but not significantly so. A high proportion of age class I individuals in the fall population is consistent with late onset of breeding. It could also indicate that the survival of late cohort (age class I) animals was high, especially in Habitats II, III and V. The proportion of age class II individuals was significantly greater in Habitat II ($G = 8.38$, $P<0.005$) in 1980 than in 1979, but not in any other habitat. This could indicate that survival to age II of age class I animals was better in Habitat II than in other habitats. A similar situation was found when age class II and III were combined ($G = 14.36$, $P<0.005$). This probably stems from the earlier onset of breeding in 1980 which allowed a greater proportion of the population to attain age class II or III by the time of fall sampling. The proportion of OW animals did not differ significantly between years or among habitats; however, most of the few OW animals

collected in the fall came from Habitat II (51% of the total in 1979, and 43% in 1980).

The proportion of mature to immature age class II animals (sexes combined) over all habitats did not differ significantly between years (P = 0.11, Fisher's Exact Test), and thus the increased density of animals in 1980 did not inhibit maturation of age class II animals.

BIOMASS

Since 79.9% of the total spring biomass and 84.4% of the total fall biomass was attributable to *C. rutilus*, the biomass of that species was analyzed to see if certain habitats supported more biomass than others. This measure is of course related to the number of animals present in a given area. If there are more animals in a given habitat then the biomass will undoubtedly be greater in that area.

SPRING:

The amount of biomass of *C. rutilus* removed from the five habitats over the three spring trapping sessions was not significantly different from habitat to habitat ($F_{(8,45)} = 1.97$, $P>0.10$, 2-way ANOVA), or from year to year ($F_{(2,45)} = 1.14$, $P>0.5$) (Appendix 9). This result is related to the fact that the spring numbers of *C. rutilus* did not differ significantly among the three trapping sessions ($F_{(2,45)} = 0.91$, N.S., 2-way ANOVA) or among the habitats ($F_{(8,45)} = 1.50$, N.S.).

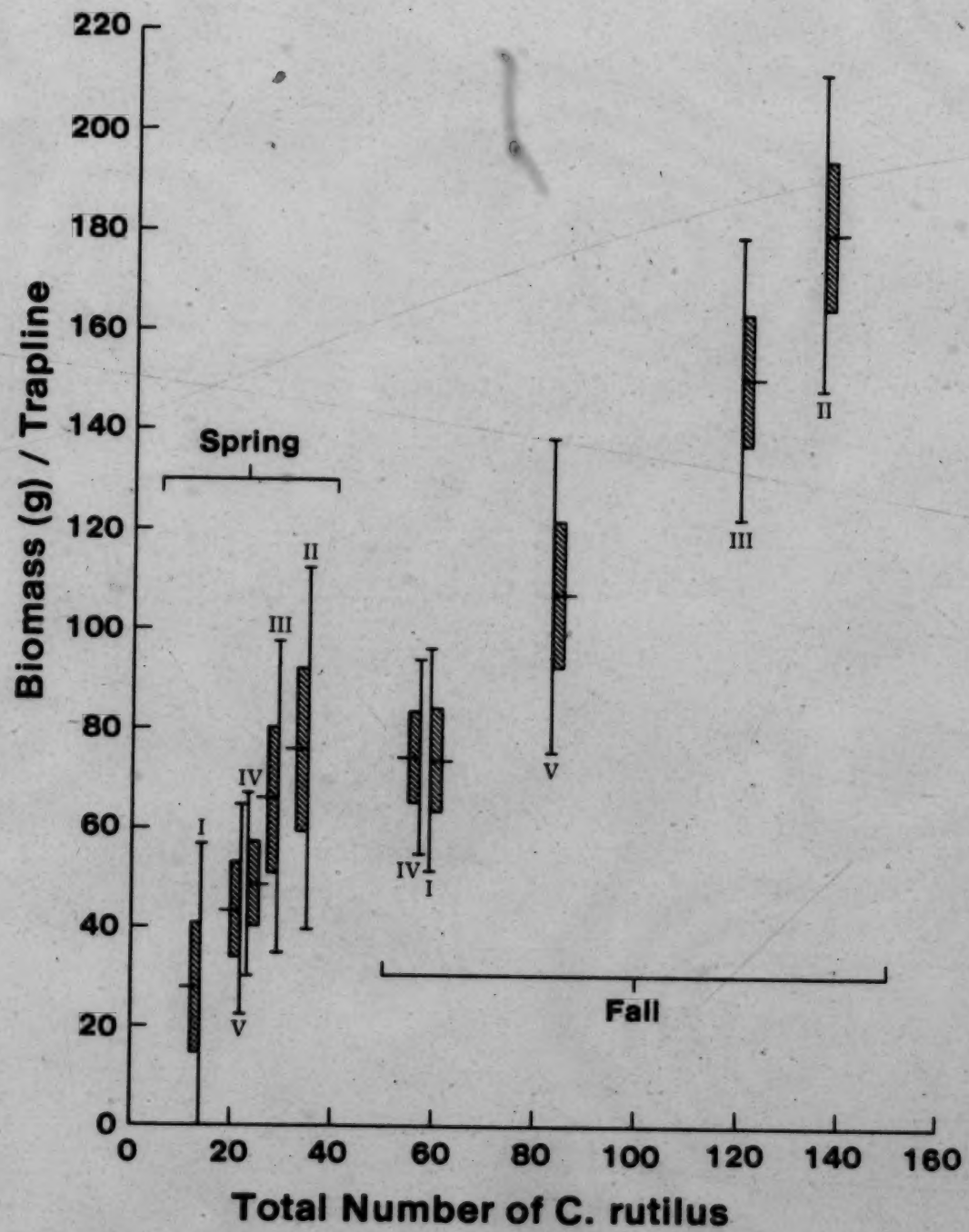
Even though biomass did not differ significantly among the habitats, certain trends were noted. Mean biomass for the combined spring captures was greatest in Habitats II and III, least in Habitat I and intermediate in Habitats IV and V (Fig. 8).

FALL:

In the fall sample, biomass differed significantly among the habitats with sexes combined ($F_{(4,75)} = 13.53$, $P<0.001$) and with sexes separate (male: $F_{(4,35)} = 6.59$, $P<0.001$; female: $F_{(4,35)} = 7.08$, $P<0.001$; 1-way ANOVA). Student-Newman-Keuls tests conducted on these data (Table 28) revealed that Habitats II and III were significantly different from Habitats I, IV and V for sexes combined and for males, and different from only Habitat I and IV for females. Assuming that habitats that support the greatest biomass of a species are superior habitats for that species, then Habitats II and III are superior to Habitats I and IV, and probably also to Habitat V.

A 3-way ANOVA (Appendix 10) confirmed that the fall biomass of *C. rutilus* differed significantly between years ($F_{(1,80)} = 21.08$, $P<0.001$) and among habitats ($F_{(4,80)} = 16.13$, $P<0.001$) but not between sexes ($F_{(1,80)} = 0.17$, N.S.). No significant difference was noted in any 2-way interaction, but a significant difference was observed in the second-order interaction of all three factors ($F_{(4,80)} = 15.62$, $P<0.001$).

Figure 8. Mean spring (1979, 1980 and 1981 combined) and fall (1979 and 1980 combined) biomass per trapline of *C. rutilus* by habitat.


Biomass (g) / Trapline
Total Number of C. rutilus
Spring
Fall
I
II
III
IV
V
0
20
40
60
80
100
120
140
160
180
200
220

The rank order of habitats, from highest biomass yield to lowest, in the fall sample was similar to that in the spring. Habitats II and III yielded the greatest biomass, Habitats I and IV the least, with Habitat V being intermediate (Fig. 8).

BODY WEIGHT AND LENGTH

Differences in body weights and lengths imply differences in animal quality; any size differences that occur may, in turn, result from differences in quality of habitats (Sheppard, 1972). Therefore, the body weights and lengths of the *C. rutilus* captured were analyzed to see if indeed animals were heavier and/or longer in any particular habitat.

BODY WEIGHTS

SPRING:

Spring body weights were compared by analysis of covariance, with date of capture as the covariate. Sex and year of trapping were analyzed separately and no significant differences in weight were found among habitats (Appendix 11).

FALL:

Fall body weights were compared by means of 2-way ANOVAS. For this series of tests the sexes were separated and the body weights of sexually mature (26.4% of age class

II and 100.0% of age class III males; 25.0% of age class II and 100.0% of age class III females) and sexually immature (73.6% of age class II males, and 75.0% of age class II females) individuals were analyzed in relationship to habitat type. As would be expected, there was a highly significant difference in mean body weight between mature and immature individuals (males: $F_{(1,118)} = 17.04$, $P<0.001$; females: $F_{(1,87)} = 156.71$, $P<0.001$) of both sexes, with mature animals being heavier. There were, however, no significant differences among habitats or in the interaction of the two (Appendices 12 and 13).

The fall sample was treated as though composed of an early cohort (age classes II and III) and a late cohort (age class I). For the late cohort, there were no significant differences in body weights among habitats or between sexes (Appendix 14). This is not entirely surprising because the animals involved were all less than 30 days of age, and thus had little time in which to respond to possible differences in quality of habitat. Significant differences in mean body weights of the two sexes were noted in mature early cohort individuals ($F_{(1,78)} = 79.33$, $P<0.001$), but not among habitats ($F_{(4,78)} = 2.15$, N.S.) or in the interaction of the two ($F_{(4,78)} = 1.03$, N.S.). Females of these age classes were consistently heavier than the males in every habitat (Fig. 9). Immature early cohort animals showed no significant differences in mean body weights (Fig. 10) between sexes ($F_{(1,125)} = 1.42$, N.S.) or among habitats

Figure 9. Mean body weights ± standard error (S.E.) and range of mature *C. rutilus* (early cohort) from the 1979 and 1980 fall trapping sessions. (N) = sample size.

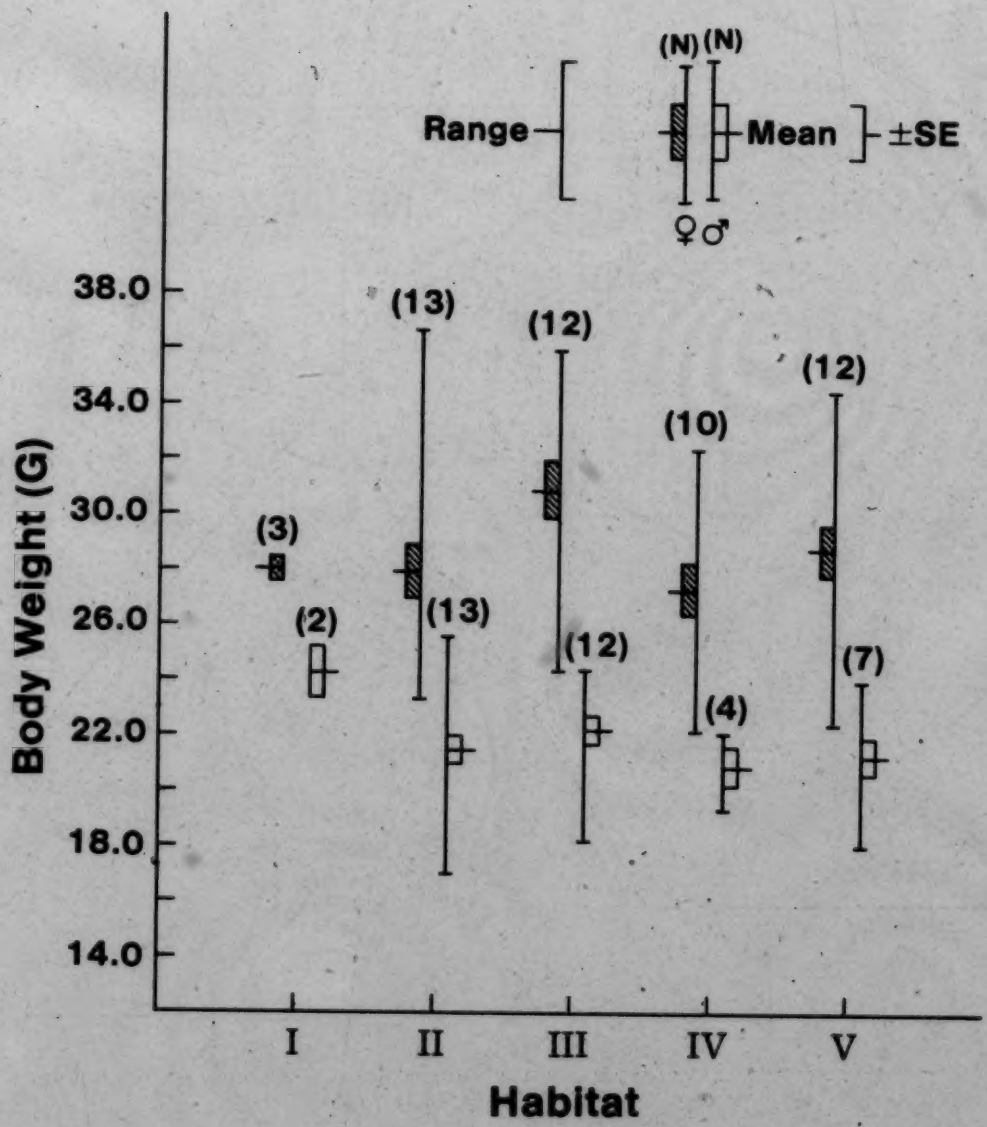
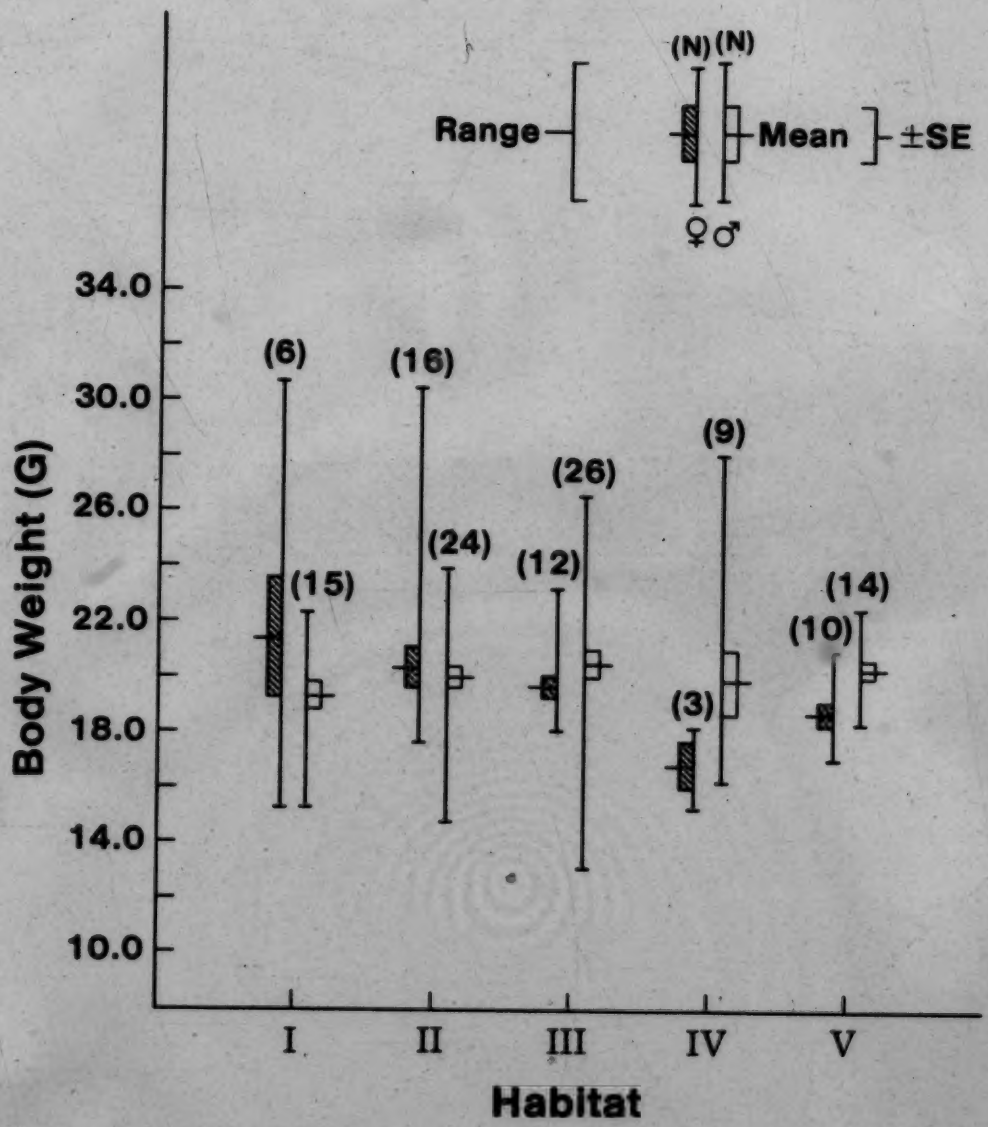

(N) (N)
Range
Mean
±SE
♀♂
38.0
34.0
30.0
26.0
22.0
18.0
14.0
Body Weight (G)
(3)
(2)
(13)
(13)
(12)
(12)
(10)
(4)
(12)
(7)
I
II
III
IV
V
Habitat

Figure 10. Mean body weights ± standard error (S.E.) and range of immature *C. rutilus* (early cohort) from the 1979 and 1980 fall trapping sessions. (N) = sample size.


Range
(N) (N)
Mean
±SE
♀♂
34.0
30.0
26.0
22.0
18.0
14.0
10.0
Body Weight (G)
(6)
(15)
(16)
(24)
(26)
(12)
(9)
(3)
(14)
(10)
I
II
III
IV
V
Habitat

($F_{(4,125)} = 1.45$, N.S.).

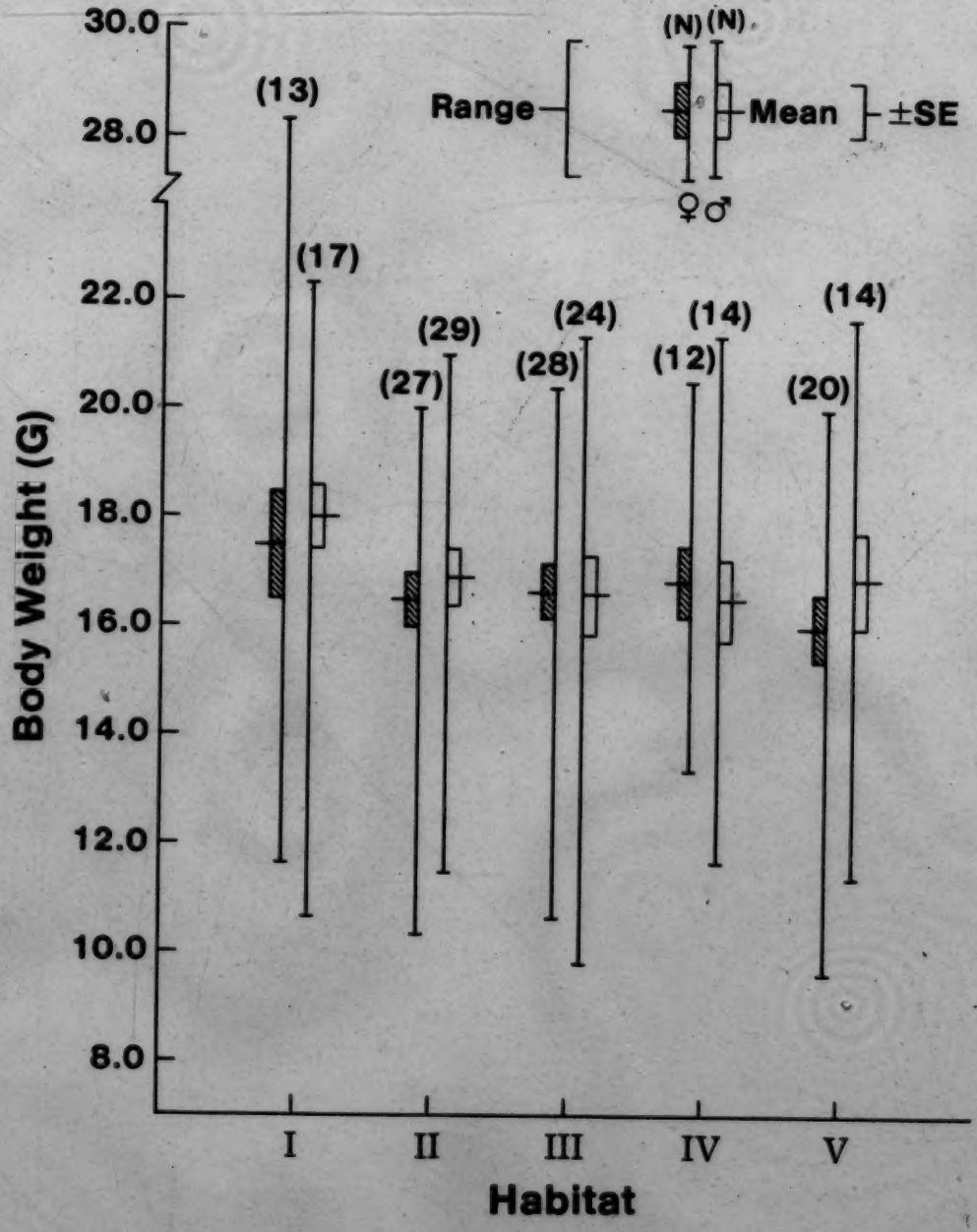
No evidence that quality of animal, as reflected in body weight, was influenced by differences in habitats was observed for late cohort (Fig. 11) individuals or immature (Fig. 10) or mature (Fig. 9) early cohort animals.

BODY LENGTHS

SPRING:

Spring body lengths (total length - tail length) were compared by analysis of covariance, with date of capture as the covariate. Since males did not differ significantly from females, either among habitats or between years ($F_{(1,113)} = 0.12$, N.S. at the $P = 0.05$ level, 2-way ANOVA with replication) sexes were combined in the analyses. Years of trapping were analyzed separately in the ANCOVA (Appendix 15) and significant differences in body length were found among habitats (1979: $F_{(4,43)} = 28.47$, $P<0.001$; 1980: $F_{(4,29)} = 37.09$, $P<0.001$; 1981: $F_{(4,32)} = 374.88$, $P<0.001$). Although the habitats did not separate out into groups when an SNK test was performed upon the 1979 data, animals from Habitats I, II and III in 1980, and Habitats II and III in 1981 (Table 29) were significantly longer than animals from the remaining habitats. Thus, habitat may influence the quality of spring-caught animals, as reflected in body length.

Figure 11. Mean body weights ± standard error (S.E.) and range of age class I *C. rutilus* (late cohort) from the 1979 and 1980 fall trapping sessions. (N) = sample size.


30.0
28.0
22.0
20.0
18.0
16.0
14.0
12.0
10.0
8.0
Body Weight (G)
(13)
(17)
(27)
(29)
(28)
(24)
(12)
(14)
(20)
(14)
Range
(N) (N)
Mean
±SE
♀♂
I
II
III
IV
V
Habitat

FALL:

The body lengths of late cohort *C. rutilus* were compared by means of two 2-way ANOVAS and no significant differences were noted among habitats ($F_{(4,190)} = 0.60$, N.S.) or between sexes ($F_{(1,190)} = 0.63$, N.S.) when the two years of trapping were combined, or among habitats ($F_{(4,190)} = 0.57$, N.S.) or between years ($F_{(1,190)} = 0.96$, N.S.) when the sexes were combined. No one habitat, therefore, produced significantly longer age class I animals of either sex in either year (Table 30).

When the body lengths of mature and immature early cohort animals were compared, the results were consistent with those found in the analysis of body weights within the same age classes. A highly significant difference in mean body length between mature and immature individuals was found in both sexes (males: $F_{(1,117)} = 7.91$, $P<0.01$; females: $F_{(1,88)} = 128.12$, $P<0.001$). However, there was no significant difference among habitats or in the interaction of the two (Appendices 16 and 17).

As with body weights, significant differences between the sexes were noted in mean body length for mature early cohort individuals ($F_{(1,78)} = 63.02$, $P<0.001$, 2-way ANOVA with replication), but not among habitats ($F_{(4,78)} = 0.53$, N.S.). The females of that cohort were consistently longer than the males in every habitat (Table 31). Immature early cohort animals showed no significant differences in mean body length (Table 31) among habitats ($F_{(4,127)} = 0.55$,

N.S.) or between sexes ($F_{(1,127)} = 2.72$, N.S.).

Thus, no evidence was found that habitat influenced the quality of fall-caught animals, as reflected by body length.

CONDITION

Body length and weight data were incorporated into a statistic called a "Condition Factor" (K) in an attempt to test for the influence habitat has on quality of animal. "In any material body in which, with increasing size, the linear proportions remain constant, weight (if density remains constant) and any bodily linear dimension are related" (Weatherley, 1972). A plot of log weight (W) in grams against log length (L) in mm yields a straight line of slope m:

$$\log W = m \log L \qquad (1)$$

Hence:

$$W = L^m \qquad (2)$$

The conditon factor is defined as observed weight (W) divided by predicted weight (L^m). For *C. gapperi* caught at Heart Lake, N.W.T. (Fuller, personal communication) and for *C. rutilus* caught in this study a value of m = 0.66 yields a mean value of about 1 for K in overwintered animals caught

in May. If observed weight is greater than predicted weight, K will be >1; if it is less, then K will be <1. Unless periods of growth in length coincide with periods of growth in weight, K will fluctuate during the life of an animal, and perhaps seasonally.

Because mean body weights did not vary among habitats whereas mean body lengths did (in spring data), there must be differences in mean K, and it is possible that any such differences will be related to habitat quality. Caution must be observed in this relationship, however, because even among the members of one population sampled on a single date, there may be considerable variation in condition for any particular length and also a change in condition with length (Weatherley, 1972).

The fall 1979 and 1980 condition factors for each age group were compared by means of 2-way ANOVA with replication. No significant differences were found in late cohort animals among habitats (males: $F_{(4,88)} = 0.67$; females: $F_{(4,80)} = 0.87$), or between years (males: $F_{(1,88)} = 0.19$; females: $F_{(1,80)} = 2.46$) (Table 32). Similarly no significant differences were found in early cohort males among habitats ($F_{(4,118)} = 0.90$); however, mature animals were in significantly better condition than immature ones ($F_{(1,118)} = 14.72$, $P<0.001$) (Table 33).

Mature early cohort females were in significantly better condition than immatures in both years ($F_{(1,87)} = 139.87$, $P<0.001$, 2-way ANOVA) (Appendix 18). A strong

separation in mean condition factor values between mature and immature animals was noted in all habitats (Table 34). A single marginal difference was also noted among habitats - mature females in Habitat III were found to be in better condition than those in Habitat IV (Table 35).

In summary then, the results of these analyses demonstrated that there was little evidence that differences in habitats influenced quality of animal. Although the condition, as measured by K, of mature early cohort females did differ significantly between Habitats III and IV at the alpha = 0.05 level, no habitat difference was found among immatures of either age or sex, or among mature males. In both sexes mature individuals had higher K values than immatures.

REPRODUCTION

FEMALES

ONSET OF BREEDING

The *C. rutilus* captured in spring revealed general trends in breeding phenology. Although females were not captured in every habitat every year, it appeared from backdating pregnancies that most conceptions took place in the first half of May. Breeding commenced subnivally in the spring each year because pregnant females were captured while some parts of the study area still had 80% snow cover. This observation is similar to that of West (1979) close to Fairbanks, Alaska (64° 15'N, 147° 43'W) in which breeding

began subnivally in the spring with no evidence of midwinter breeding. I detected no difference in date of onset of breeding among habitats, in spite of differences in snow conditions (Table 36).

Of the 51 *C. rutilus* females captured in the pooled spring trapping sessions, 43 or 84.3% were either pregnant or had placental scars, indicating that they had just given birth to a litter. Two individuals possessed both embryos and placental scars, but were caught in mid-June 1979 in those habitats (III and IV) that were the last to be trapped.

AGE AT MATURITY

Forty-two female *C. rutilus* were captured during the summer and the proportion of the various age classes that matured were as expected (Burns, 1980; Dickinson, 1976). One hundred percent (N = 17) of the OW females captured were mature as judged by the presence of either embryos or placental scars. Those caught in June had either embryos or one set of placental scars, not both, but those captured subsequent to that had either embryos and scars present in the uterus or had two sets of scars. Most (8) of the age class II and III (N = 10) were mature. They first appeared on 18 July with either embryos or one set of placental scars.

One-third of age class I females (N = 15) matured in the summer of their birth. Those that did mature were members of the first litters of the OW animals and were all

captured in a narrow window (14 - 19 July).

Since the breeding season had all but ended by the time the fall trapping campaign commenced, very few pregnant females were captured. Placental scars, indicating past reproductive activity, were present in all of the OW (N = 15) and age class III females (N = 34), 25% of age class II females (N = 64) and none of the age class I individuals (N = 102). Since maturity was an "all or none" phenomenon in 3 of 4 age classes, only age class II could vary among habitats. No significant difference was found, however, among the habitats in the proportion of age class II females that matured, indicating that the proportion mature was independent of habitat type.

NUMBER OF LITTERS PER FEMALE

With the age classes in fall samples from habitat trapping combined there was no significant inter-year difference ($F_{(1,8)} = 3.14$, N.S.) in the number of litters produced (2-way ANOVA). Therefore, the data for both years were pooled in a 2-way ANOVA (Appendix 19) and no significant difference in number of litters was revealed among age classes ($F_{(2,14)} = 2.81$) or habitats ($F_{(8,14)} = 1.63$).

When samples removed from live-trap lines in September 1980 were combined with samples from habitat trapping, 79.2% (N = 19) of the OW *C. rutilus* females that had survived to September had given birth to at least two litters, (two sets of recognizable scars or pregnant with one set of scars)

(Table 37). The reverse trend was observed in age class II, in which 27.3% of the mature females (N = 22) had had two litters, while most (72.7%) had had only one. In age class III females, 52.6% (N = 57) had had two litters, whereas 47.4% had had one. Only one female was thought to have had more than two litters in the course of the study. This was an OW individual captured in Habitat III in the fall of 1980, but the third set of placental scars was so faint that an accurate count could not be made. Dickinson (1976) and Fuller (1969) also found that one or two litters were normal, three exceptional.

LITTER SIZE

The mean number of young per litter did not differ significantly among habitats in the total spring trapping effort ($F_{(4,43)} = 0.67$, 1-way ANOVA, Table 38). The mean number of young per litter in the spring (mean = 4.28, N = 45) was significantly less than the mean number in the last litter of the three mature age classes in the fall (mean = 6.55, N = 111) ($t = 6.38$, $P<0.001$).

The size of the last litter was compared across habitats by means of a 1-way ANOVA, and of the three mature age classes only the mean litter size of age class III showed any significant difference ($F_{(4,58)} = 2.57$, $P<0.05$). An SNK test performed upon these data revealed that litters from Habitat IV were significantly larger than those from Habitat I (Table 39).

As expected (Dickinson, 1976; Stenseth *et al.*, 1980), the older, heavier, overwintered females gave birth to significantly larger litters (mean = 8.46 ± 0.47, N = 25) than the younger, lighter age class II (mean = 5.86 ± 0.43, N = 26) and III (mean = 6.26 ± 0.28, N = 60) females (t-tests: OW versus II, $t = 5.03$, $P<0.001$; OW versus III, $t = 3.94$, $P<0.001$). The mean litter size of age class II did not differ significantly from that of age class III ($t = 1.16$, N.S.). Age class II and III combined had smaller litters than OW females ($t = 4.46$, $P<0.001$).

In those females that had two litters during the breeding season (Table 40), the second litter was usually larger than the first; however, it was not significantly different at the $P = 0.05$ level (OW: $t = 0.29$; age class III: $t = 0.41$; age class II: $t = 0.44$). A difficulty arises in this analysis, however, as the number of placental scars for the earlier litters may not be clearly visible, and hence an inaccurate count may be obtained, which errs in the direction of a smaller number of young per litter (Dickinson, 1976). For the purposes of this study, the number of young per litter was assumed equal to the number of placental scars seen.

The mean size of the first litter did not differ significantly among the three age classes ($F_{(2,52)} = 1.93$, N.S., 1-way ANOVA). Significant differences, however, were noted in the mean size of the second litter ($F_{(2,37)} = 7.37$, $P<0.005$) with the OW females producing larger second litters

(mean = 8.58, N = 20) than either age class II (mean = 6.00, N = 6) or age class III (mean = 6.33, N = 32) females. No significant differences in litter size were found between age classes II and III (SNK test).

The average output of embryos per female for the combined fall sample was calculated (Table 41) and the totals did not differ significantly from habitat to habitat (chi^2 = 1.07, 4 d.f.). Even though the reproductive output varied among age classes, the average output of embryos per female of all age classes, differed little among habitats. The total weighted average output of embryos is higher in Habitat IV than in other habitats due to the proportion of age class III and OW females in this habitat. Therefore, fewer females produced larger litters in this habitat type, as has been discussed for the last litter. An estimate of the total reproductive output per habitat can be calculated by multiplying the number of mature females of different age classes by the mean number of litters/100 trap nights and mean litter size. No significant difference (chi^2 = 2.20, chi^2 test) was noted among the five habitats when the number of young/100 trap nights was compared; however, the greatest reproductive output was in Habitats II and III (8.65 and 6.99 young/100 trap nights respectively), with Habitat I possessing the least (3.57). Habitats IV (5.75) and V (6.35) were intermediate.

LENGTH OF BREEDING SEASON

According to Dickinson (1976), the frequency of litters is in part related to the onset of the breeding season. Breeding commenced during the first two weeks of May in both 1979 and 1980, and ended at the end of August - beginning of September for a total breeding season (first to last conception) of 120 and 115 days for 1979 and 1980 respectively. The length of the breeding season observed by West (1979) in Alaska (64° 51'N) was very similar to that found in this study, in that *C. rutilus* breeding began in early May and ceased in early to mid-September. Martell (1975) found a breeding season for *C. rutilus* lasting 119 days at a latitude of 69°N, which is similar to the breeding season lengths found in this study.

MALES

Every OW male captured in the spring was mature (Table 42). Fifty percent of the age class I males captured (N = 24) during the summer months of June, July and August were mature. All were caught in July. Young males caught in June (first appearance 26 June) had not had time to mature, and no individual of age class I in August was mature. Most (72.0%) age class II and III males captured (N = 25) were mature. Although age class II animals should have been in the population in late June, their first appearance in samples was on 17 July. All OW males captured during the summer trapping period were sexually mature.

Few (N = 14) males still in breeding condition were found in the September samples, but males with regressing testes and accessory glands still obvious were taken. Only 1.4% of 139 age class I males in the fall sample had matured. All OW and age class III males had matured and 34.0% of 198 age class II males were found to have been mature. The proportion of mature males, in age class II, differed significantly among habitats ($G = 10.12$, $P<0.05$). There was a significantly greater proportion of mature males in age class II in Habitats II ($G = 5.63$, $P<0.05$) and III ($G = 9.68$, $P<0.005$) than in Habitat I. Habitats IV and V were not significantly different from Habitats II and III.

In general, the results obtained from the sample of males in the fall mirror those of the females. Individuals of both sexes that were still in age class I in September failed to mature (with the exception of 1.4% of the males). Most age class II individuals also failed to mature, but males matured at a higher rate than females (33.8% versus 20.6%), which is contrary to most reported results for *C. rutilus* (Kalela, 1957; Koshkina and Korotkov, 1975). All age class III and OW animals were sexually mature.

The last scrotal male captured was on 15 September in 1979 and 12 September in 1980, which indicates that the male breeding season ended at much the same time over the two years. Since all males were sexually mature and scrotal at the commencement of spring trapping in early May, the breeding season is approximately 4.5 months in length.

LIVE TRAPPING

During the two years of study, 7050 trap nights yielded 517 captures of 226 different *C. rutilus*, 1 *Synaptomys borealis* and 1 *Microtus longicaudus*. No animals marked in 1979, the first year of trapping, were recaptured in 1980, probably because of the small number (50) marked in 1979, and a reduction of the number of transects trapped from 4 in 1979 to 2 in 1980.

Since a vegetation survey was conducted at each live-trap location, the habitat at each trap site could be determined. By recording the frequency of captures and comparing it with expected frequency, one could then determine which habitat types supported the greatest abundance of animals. The expected number of captures was determined by multiplying the total number of captures over all habitats by the percentage of traps in that particular habitat. The 517 captures were not distributed equally among the five habitats (G-test of independence, $G = 90.64$, $P<0.001$), which indicates a preference for certain habitats.

Having found that the captures were not in proportion to what was expected among the habitats, pairwise comparisons using the G-test were conducted to determine which habitats were preferred by *C. rutilus*. Significantly more total captures were observed in Habitat III than Habitat II ($G = 11.83$, $P<0.005$) when the expected number of captures was compared with the observed number of captures. Habitats I and IV were not significantly different in the

expected number of captures from each other (G = 1.60), as were Habitats IV and V (G = 1.99). The number of captures in Habitat I did differ significantly from the number in Habitat V (G = 5.51, P<0.025), which had the fewest captures. The apparent low abundance of *C. rutilus* in Habitat V may have been a result of insufficient trapping effort -- only 22 trap stations of a total of 340 (6.5%) were located in Habitat V. The majority (65.7%) of the captures/100 trap nights were in Habitats II and III, with Habitat V the least (6.3%) and Habitats I (13.5%) and IV (14.5%) intermediate (Table 43).

It was not possible to determine home ranges or densities of *C. rutilus* because of the design of the study. However, some indication of mobility was obtained. The greatest distance between captures for an individual was approximately 145 m (6 trap intervals). The majority (78.5%) of the marked voles were not recaptured more than one trap interval from the point of marking.

Live caught animals were placed in weight classes rather than age classes. Class 1 individuals weighed <18.0 g, and were probably mainly age class I. Class 2 individuals weighed 18.1 to 25.9 g and were mainly members of age classes II and III. Those over 25.9 g were placed in Class 3 and were considered to be mainly OW. Early in the season no young of the year had attained 26.0 g in weight, but by August, some young in snap-trap samples had done so and it was no longer possible to recognize OW animals with complete

confidence. Class I animals began appearing in Habitats II and III during the third rota (7 - 10 July), and Class 2 individuals first made their appearance on the live-trap lines in rota four (21 - 24 July).

Class I individuals comprised 47.6% of the total catch and Class 2 animals 50.0% in the sixth and final live-trapping rota (N = 82). Of a total of 238 animals in the seventh rota (where snap-traps were used), only 28.6% had been previously marked. The remaining 71.4% was composed mainly of age class I and II animals that had previously evaded capture, or had only recently emigrated into the area.

Sex ratios in the sample removed from live-trap lines were similar to those from the index trapping of habitats. The proportion of males to females in age class I was not significantly different from 1:1 (Gp = 0.86). Males exceeded females in age class II (Gp = 9.77, $P<0.005$) with almost twice as many males as females taken (Table 44). A highly significant difference (Gp = 17.40, $P<0.005$) was noted in the sex ratio of age class III, in which females greatly outnumbered males. When age classes II and III were combined, no significant difference from a 1:1 ratio (Gp = 1.35, N.S.) existed. With these two age classes combined (N = 146) the proportion of males (55.0%) is similar to the proportion of males found in age class I (56.0%).

DISCUSSION

CRITERIA FOR HABITAT PREFERENCE

Habitat selection or preference by an animal by definition is "The choice of a type of place in which to live" (Partridge, 1978) and has been discussed by several authors where choice has been shown to be involved, with examples involving iguanid lizards (*Sceloporus jarrowi*; Simon, 1975), the great tit (*Parus major*; Royama, 1970), jaegers and owls (Pitelka, *et al.*, 1955), snowy owls (*Nyctea scandiaca*; Lein and Webber, 1979), several species of forest birds (Alatalo, 1981), wild ruminants (Hudson, 1976; 1977), including the impala (*Aepyceros melampus*; Pettifer and Stumpf, 1981), bobcats (*Lynx rufus*; McCord, 1974), the red fox (*Vulpes vulpes*; Jones and Theberge, 1981) and numerous examples among small mammals (see Introduction).

The criteria used by other authors to indicate whether small mammals select or prefer certain habitats are often sketchy. The criterion used by Douglass (1976) was the amount of time 2 species of *Microtus* spent in a given habitat. This measure, as well as the rate of travel in each habitat and the average penetration of individuals into different habitats, were considered by Wecker (1963) in a study of habitat selection by *P. maniculatus*. Although rarely stated, it appears that number of animals and their

presence in, or absence from, a given habitat are the criteria most authors use to quantify habitat selection.

Since precisely defined guidelines for the determination of habitat preference by small mammals were lacking in the literature, certain criteria were devised in this study in an attempt to determine whether individuals of *C. rutilus* express habitat preference. These criteria included the relative number (catch per unit of effort) of animals within the different habitats, and several indices of animal quality - body weight, body length, condition factor and reproductive output. Under the null hypothesis that all habitat types support the same number and quality of individuals, there would be no advantage to selecting a particular habitat type. Habitat selection would be of value if different habitats support different densities of individuals, or individuals of different quality.

It is a long held belief that if a small mammal species is found in an area or habitat in a greater abundance than in another area or habitat it is because that animal prefers the optimal area or habitat (Findley, 1951; Quast, 1954; Wecker, 1963; Grant, 1971; Kirkland and Griffin, 1974; Douglass, 1976; Dueser and Shugart, 1978; Partridge, 1978). Animals can be forced into suboptimal habitats due to inter- or intra-specific competition, or they can select habitats with few competitors. Intraspecific interaction associated with high density in one habitat could be a reason for animals to select other habitats where competition and

possibly even predators are absent, as was observed by Grant (1971) for *M. pennsylvanicus*.

Studies concerning habitat preferences of other small mammal species revealed that small mammals prefer a variety of habitats for a variety of reasons. Morris (1955) and Richens (1974) concluded that dense ground cover, fallen trees, decaying logs, slash, heaved-out roots and stumps all contribute to high small mammal densities. Morris (1979) indicated that species density of small mammals in southwestern Ontario was significantly correlated with the depth of dead grasses, leaves and other debris on the soil surface. Mean foliage height diversity was correlated with species density, whereas most measures of horizontal habitat heterogeneity were not good predictors of species numbers (Morris, 1979).

The white-footed mouse, *Peromyscus leucopus*, occurred at sites with primarily deciduous canopy, low density of trees, high density of shrub-understory vegetation and low shrub evergreenness, in a study in eastern Tennessee by Dueser and Shugart (1978). The association of *P. leucopus* with relatively high density of shrub-understory vegetation was reported by other authors (Klein, 1960; Getz, 1961; Smith and Speller, 1970; Myton, 1974; M'Closkey, 1975). The golden mouse, *Ochrotomys nuttalli*, occurred at locations with dense ground cover and denser than average undergrowth and with primarily evergreen canopy (Dueser and Shugart, 1978).

The woodland jumping mouse, *Napaeozapus insignis*, responded to a factor (s) other than the dominant vegetation (Kirkland and Griffin, 1974). Whitaker (1963) and Brower and Cade (1966) noted a positive response of *N. insignis* to ground cover which is generally lacking in well-shaded coniferous areas. Cover by wedgeleaf ceanothus (*Ceanothus cuneatus* (Hook.) Nutt.) was the preferred habitat of *Peromyscus truei* (Quast, 1954) and if ceanothus was absent, this species used rock habitats sheltered by live oak bushes, a habitat that more generally produced *Peromyscus boylii*. Quast (1954) also observed that the tulare kangaroo rat, *Dipodomys heermanni tularensis* (Merriam) was associated with bare or nearly bare soil and was not found in areas of tall grass or heavy grass litter. Its greatest abundance occurred on bare soil under the protective canopies of ceanothus bushes (Quast, 1954). Unlike *D. heermanni*, *M. pennsylvanicus* displayed a positive correlation between population density and amount of graminoid cover (Eadie, 1953; Mossman, 1955; Zimmerman, 1965; Getz, 1966).

The northern redbacked-vole, *Clethrionomys rutilus* (Pallas), occurs throughout the Eurasian taiga and the mainland tundra and taiga of northwestern North America. Taiga populations have been studied in Alaska (Pruitt, 1968; Whitney, 1976; 1977; West, 1979; 1982), Northwest Territories (Martell, 1975; Dickinson, 1976; Burns, 1980) and the Soviet Union (eg. Koshkina and Korotkov, 1975). The possibility exists that different demographic patterns hold

for *C. rutilus* in northern and southern portions of its geographic range (West, 1982). The effect of varying environmental factors on *C. rutilus*, and the idea that intra-specific demographic features should vary in response to different environmental conditions, have been studied by some authors (Koshkina and Korotkov, 1975; Lidicker, 1978; Martell and Fuller, 1979).

Two central Alaskan studies, near the center of the North American range of *C. rutilus*, Whitney (1976; 1977) and West (1979; 1982) shed light on habitat selection by *C. rutilus*. *Clethrionomys rutilus* has been called the "*Peromyscus* of the north" (Guthrie, 1965 in Whitney, 1976) because they live in a great variety of habitats: north- and south-facing spruce associations; all types of birch, poplar, and alder associations; bogs and creek beds (Whitney, 1976). West (1979) referred to *C. rutilus* as a "habitat generalist" due to its occurrence in practically all (98.0%) of the sites he trapped, while Whitney (1976) considered *C. rutilus* to have "a broad niche". The results from my study agree with the earlier findings of Whitney (1976) and West (1979). *Clethrionomys rutilus* was the numerically dominant small mammal species captured, and was present in every habitat type on the study area.

Concerning the biology of *C. rutilus*, most authors (ie. Koshkina and Korotkov, 1975; Martell, 1975; Whitney, 1976; West, 1979) agree that a typical year starts with a breeding population in late April or early May composed of

overwintered animals born mostly in the previous August. These voles produce up to three litters before breeding stops in late August early September. All of the first litter matures, a variable proportion of the second litter matures, and none of the third litter matures. Young of the first two litters produce one or two litters, but none of these second generation voles mature until the start of the next breeding season.

Both Khlebnikov (1970) and Whitney (1976) observed subnivean breeding in the winter and early spring, which is contrary to this study and that of West (1979), where no evidence of winter breeding was observed. In their study of *C. rutilus* in Siberia, Koshkina and Korotkov (1975) maintained that the timing of spring reproduction and the rate of maturation of the spring cohort are correlated with the spring density of overwintered females. Low spring density of overwintered females resulted in early reproduction and early maturation of the first cohort, whereas high spring density of overwintered females was followed by late onset of breeding and late maturation of the first cohort. Weak support was found for this hypothesis by Fuller (1979) for Canadian populations of *C. gapperi*, West (1982) for Alaskan populations of *C. rutilus* and in this study for Yukon populations of *C. rutilus*. Neither the onset of spring reproduction nor the number of reproducing first generation females was related closely to spring density of overwintered females. All first generation

females matured quickly and bred.

The *C. rutilus* population studied by West (1982) followed an annual cycle of abundance in contrast to the multiannual pattern proposed by Pruitt (1968). Whitney (1976) also concluded that the population of *C. rutilus* he studied near Fairbanks exhibited an annual cycle of abundance. West (1982) suggested that consistency is not found in peak fall densities, as Whitney (1976) concluded, but rather in the annual periods of low density characteristic of spring and early summer. This observation is consistent with that of this study where spring densities were similar over three years. Thus, in central Alaska (West, 1982) and in south-central Yukon, *C. rutilus* undergoes a marked annual cycle with variable peak fall density. The determination of whether peak fall densities occur at intervals of 3 - 4 years, or at irregular intervals will require longer-term studies than the one conducted here.

THE "IDEAL" HABITAT

Habitat studies involving *Clethrionomys* spp. indicate that the distribution of *C. gapperi* was closely correlated with the presence of stumps, rotting logs and root systems in loose forest litter and sphagnum moss (Gunderson, 1959), depth of dead grass, leaves and other debris (Morris, 1979), and fallen trees and limbs, stumps, brush piles and boulders

(Miller and Getz, 1972). Kirkland and Griffin (1974) concluded that *C. gapperi* responded to factors other than dominant vegetation, and suggested water as the probable factor. Butsch (1954, in Gunderson, 1959) and Miller and Getz (1972; 1973) indicated that the local distribution of *Clethrionomys* appeared to be controlled by the availability of free water. Gunderson (1959), however, concluded that the availability of free water was not a limiting factor in *Clethrionomys* distribution in his study area (Cedar Creek Forest, Anoka County, Minnesota). *Clethrionomys gapperi* appeared to be more abundant in areas with greater debris cover owing to increased protection from predation. The amount of vegetative cover may also modify other environmental factors such as microclimate at the surface as well as soil moisture and temperature (Getz, 1970). Data concerning the importance of these factors in habitat preference are limited in the literature.

Few studies have dealt with habitat preferences of *C. rutilus*. West (1979) discussed *C. rutilus* habitat responses to central Alaskan forest succession; Burns (1980) analyzed habitats of *C. rutilus* on islands in the Mackenzie River and Martell (1975) studied the demography of tundra and taiga *C. rutilus* in the Northwest Territories, Canada.

If the ideal habitat for small northern mammals were to be described on the basis of those characteristics found in the literature, it would consist of a mature forest (Iverson and Turner, 1973) with fallen trees and foliage cover (Dyke,

1971) and logs (Miller and Getz, 1972; 1973). There would be high density and diversity of shrubs (Iverson and Turner, 1973; Green, 1978) and brush piles for protection from predators and from the elements (Miller and Getz, 1972; 1973; Green, 1978). Sufficient quantities of food would be present in the form of fruits, seeds, mushrooms and chlorophyllous material (Dyke, 1971; Vickery, 1979), overwintered berries (West, 1982) and thick moss for both consumption and bedding material (West, 1977).

When the habitats in this study are compared with the "ideal" small mammal habitat and ranked in order of what should be the most appealing to small mammals, Habitats II and III were clearly the most similar to the "ideal". With regard to forest age, Habitats II and III were the oldest and most mature, with an age greater than 170 years. Much debris in the form of fallen logs, trees and branches was present in Habitats II and III; very little was in Habitat I, and varying amounts occurred in Habitats IV and V. Habitats I and IV however, possessed the highest shrub abundance (Table 11), (which is desirable from a *C. gapperi* point of view (Iverson and Turner, 1973; Green, 1978)).

Food is certainly of major importance in any consideration of growth (Krebs and DeLong, 1965; Batzli and Cole, 1979; Cole and Batzli, 1979; Batzli and Jung, 1980; Krohne, 1980) and with regard to the diet of *Clethrionomys* spp. and *C. rutilus* in particular, a study of the major food items present within the habitat types reveals that

preferred foods were present in varying amounts in all habitats. Availability and abundance of major food items are important in the selection or preference of habitats by small mammals (Gunderson, 1959; Zimmerman, 1965; Meserve, 1976(a),(b); Holbrook, 1978; Vickery, 1979; Batzli and Jung, 1980) and large mammals (Petrides, 1975).

Although analysis of stomach contents was not part of this study, *Clethrionomys* spp. are known to eat large quantities of a limited number of fruits as well as seeds, mushrooms, chlorophyllous material and arboreal lichens (Dyke, 1971; Vickery, 1979). Kalela (1957) found that the shoot tips and leaves of *Betula*, *Empetrum nigrum*, *Vaccinium uliginosum* and *Vaccinium vitis-idaea*, the green parts of *Cornus* sp., *Pedicularis* sp., *Solidago* sp., *Viola* sp., *Linnaea borealis*, *Rubus* spp., *Pyrola* sp., and *Petasites* sp. were important summer food species for *C. rufocanus*. These genera plus other fruit- or seed-producing plants were present in varying amounts in the habitat types (see Vegetation Results). Habitat III had a great abundance of several of the fruit- or seed-producing genera, as did Habitat V (Tables 11 and 12), whereas the abundance was not as great in the remaining habitats.

Clethrionomys gapperi (Dyke, 1971) and *C. rutilus* (West, 1979) consume ground lichens only during winter and spring; thus, those habitats with an abundance of lichens (ie. Habitats I, II and III) may constitute superior overwintering places. Berries that overwinter (ie. *E.*

nigrum, *Arctostaphylos uva-ursi*, *Geocaulon lividum*, *V. uligonosum*) are important food resources in the spring prior to the growth of new shoots and leaves and before the current berry crop has matured (Dyke, 1971; West, 1979). According to West (1982), *C. rutilus* in central Alaska depend upon berries as food during winter. Fruit-bearing plants in central Alaska, and in this study, typically flower in June and July and produce berries in late summer and fall, resulting in a superabundance of food in the fall. Before this food resource can be exhausted by small mammals, birds and insects, it is covered by snow. It then becomes the exclusive property of small mammals because it is concealed from birds, insects become inactive, and decomposition is essentially halted at prevailing subnivean temperatures. Thus, fall berry production usually supplies a substantial food supply throughout winter and early spring.

Concerning the species of overwintering berries found on the study area, Habitats I and IV appeared to have the greatest abundance with Habitats II and III the least (Tables 11 and 12). Even though Habitats II and III possessed fewer berries than other habitats, the amount present may be sufficient to supply food during the winter to the small mammal population. It is possible that winter preference is different from summer preference and the animals move from habitat to habitat, but only summmer use was measured in this study.

West (1979) suggested that moss consumption prior to growth of new summer vegetation was important to *C. rutilus*, but whether it is indicative of limited food availability in early summer or a matter of preference requires further investigation. If indeed moss is an essential component of the winter diet of *C. rutilus* then those habitats with an abundance of moss species would be superior to those lacking mosses. In addition to its value as food during winter, a sufficiently thick layer of moss may also be important as an area for escape from predators, and for conservation of energy and the extra insulation it provides under conditions of persistent cold (West, 1977). In my study area, however, all habitat types but Habitat I contained a substantial moss layer (from 48% to 83%; Table 13).

With great consistency the greatest abundance of *C. rutilus* was found in Habitats II and III; the least abundance was recorded for Habitats I and IV, with Habitat V usually intermediate. The amount of *C. rutilus* biomass removed from the various habitats mirrors the relative abundance of voles captured in those habitat types. Since more voles were captured in 1980, the biomass value was greater in that year than in 1979.

Small rodent distributions, particularly those of microtine rodents, have been shown to be closely related to the type and amount of vegetative cover (ie. Eadie, 1953; Mossman, 1955; Hodgson, 1972; Birney *et al.*, 1976). Habitats II and III consisted of the most mature, least disturbed

forest in my study area. Iverson and Turner (1973) found the greatest abundance of *C. gapperi* in mature forests. Habitat II however, had the lowest shrub diversity of any of the habitats, which is contrary to the findings of Iverson and Turner (1973) who found that areas with great shrub diversity had more voles than those of less shrub diversity. They go on to say however, that it is not known what the importance of shrub diversity is to the animals.

Miller and Getz (1972; 1973) concluded that the primary factor influencing the local distribution of *C. gapperi* was the amount of cover available in the form of fallen trees and logs, brush piles, and rocky areas. In a few places, cover from low conifer limbs may act in a similar manner (Miller and Getz, 1972). Protection from predation is assumed to be the primary reason for high abundance in sites with much cover (Miller and Getz, 1972). Habitat II consists of mature *A. lasiocarpa* forest which is the oldest on the study area (>175 years) and consequently contains much fallen debris and many downed trees. Habitat I on the other hand, consists of very few downed trees and little debris as it is composed of young *P. contorta* trees of less than 95 years or between 105 - 160 years of age (Archibald and Russell, 1979).

Green (1978) suggested that species composition and density of the shrub understory, density of ground cover, accumulation of leaf litter and the presence of deadfall were important habitat components associated with high

numbers of *C. gapperi*. The shrub canopy in Habitats I and IV was composed primarily of *Salix* spp. and young *A. lasiocarpa* which were associated with low numbers of *C. rutilus*. The presence of these shrub species and habitat factors associated with them may explain the low numbers of *C. rutilus* in these two habitats. Similarly, the lack of a substantial shrub understory (shrubs less than 2 m tall), as in Habitat I, limited litter accumulation and the lack of deadfall in this habitat may also explain the low abundance of *C. rutilus*. Conversely, the presence of *Betula*, *Empetrum*, *Ledum* and *Vaccinium vitis-idaea* in addition to *Abies* and *Salix* in the shrub canopy may explain the relatively high abundance of voles found in Habitats II and III, and to a lesser extent in Habitat V.

Habitat I was the driest habitat, which may cause it to be avoided by *C. rutilus*. Getz (1968) has shown that *C. gapperi* has a high water requirement because of a relatively inefficient kidney, and the same may be true of *C. rutilus*. If so, most *C. rutilus* would be expected to occur only in those habitats in which free water is available, or where adequate water can be obtained in its food (Miller and Getz, 1973; Gunderson, 1959). Although water availability was not measured during the study, standing water was observed throughout the summer in all habitats but Habitat I. Mosses were also observed to assist in retaining water after rains. Habitat I had very little moss (approximately 7% cover; Table 13).

Snow cover could play an important role in explaining greater abundances of voles in areas of deep and prolonged snow cover (Formozov, 1946; Pruitt, 1957; Fuller, 1967; Whitney, 1976; 1977; West, 1982). In upland sites, such as Habitat II, the snow lasts longer in the spring than in any other habitat and thus could provide an extended period of protection from predators for the voles before the growth of new vegetation. If moisture and cover were limiting factors in preventing the establishment of voles in certain areas, one might expect the species to move into upland sites when snow was present during the winter months. The snow could presumably be used as a direct source of moisture and would also afford protection from predation (Miller and Getz, 1972).

Since *C. rutilus* appears to be a habitat generalist (West, 1979) and was the most abundant murid in all habitats, it would seem reasonable that competition with other species of small mammals is not a major factor in its habitat preference. In my study area, the only habitat in which interspecific competition may occur is Habitat V, where 17.6% of the fall catch consisted of *M. pennsylvanicus*, the second most abundant murid. *Microtus pennsylvanicus* is a grassland species (Hodgson, 1972; Birney *et al.*, 1976; West, 1979); however, it has been shown to be capable of living in forests (Cameron, 1964; Clough, 1964; Morris, 1969). Of all *M. pennsylvanicus* captured (N = 34), 91.2% came from Habitats IV and V, perhaps because these

habitats had the greatest cover of grasses. The lack of *Microtus* in habitats lacking open grassy areas reinforces the view that in boreal forest, trophic specialization restricts the range of suitable habitat for *Microtus* (West, 1979).

The black spruce forest (Habitat V) was considered mature (Russell, personal communication) and as such, according to Iverson and Turner (1973), should have contained a high abundance of *C. rutilus*. Competition with *M. pennsylvanicus* (Cameron, 1964; Clough, 1964; Grant, 1970) or deficiencies in habitat quality could, quite possibly have prevented *C. rutilus* from reaching and maintaining high numbers in Habitat V.

Calhoun (1963) suggested that in a given habitat some species may be dominant over others and prevent them from entering traps until the dominant species has been removed. Few members of other small mammal species were captured subsequent to the removal of *C. rutilus* from the area at every trap check, during the snap-trapping campaigns; therefore, it is unlikely that the presence of *C. rutilus* prevented other species from entering the traps. It is also unlikely that other species prevented *C. rutilus* from entering traps because even in habitats of few *C. rutilus* (ie. Habitats I and IV) there was not a greater capture success of other small mammal species, except the aforementioned *M. pennsylvanicus* captures in habitat IV.

DEMOGRAPHY OF *C. rutilus* WITH REGARD TO HABITAT RELATIONSHIPS

Few studies have been undertaken, and consequently little information is available, concerning demographic parameters of *Clethrionomys* in relation to habitat preference. Therefore, with regard to the second measure of habitat preference, few comparisons can be made between the findings of this study and those of the literature.

Body size is a quantitative measure of response to environmental conditions and habitat quality, and as such was analyzed to determine if body size varied among habitats. No indication that habitat differences had any effect on the body weights of either sex of *C. rutilus* was observed. Mature voles were significantly heavier than immature animals, as would be expected, but this difference was not habitat specific.

Body length, on the other hand, did differ among habitats. The mean body lengths of spring-caught voles found in Habitats I, II and III in 1980 and Habitats II and III in 1981 were significantly longer than those of voles in the remaining habitats (Appendix 15, Table 29). Length, which is a measure of skeletal development, is more likely to reflect a genetic difference than is weight, which is easily influenced by environmental conditions. However, length in spring may also be a function of winter conditions, especially the thermal regime in the subnivean environment (Formozov, 1946; Pruitt, 1957). I have very little

information concerning snow cover and depth in this study; however, snow lasted longer in upland sites, such as Habitat II and the higher elevations of Habitat III. In addition to providing an extended period of protection from predators (Miller and Getz, 1972), the persistent snow cover could also have allowed the animals in those areas exclusive access to overwintered berries (West, 1982), thus facilitating growth.

Spring temperature is the primary determinant of the date of disappearance of the snow cover, and in concert with photoperiod, initiates new vegetative growth. The combined action of snow cover, light, and food probably influences the growth of microtine rodents in early spring. Habitat differences did not seem to influence the quality of fall-caught *C. rutilus* as reflected by body length, which indicates that all habitats supported growth during summer, regardless of the abundance of animals in those habitats.

The use of certain habitats by small rodents and differences in vegetation among the habitat types may reflect the quality and availability of food to *C. rutilus* and in turn, may influence the condition (K) of small rodents in these areas. According to this measure of condition, the condition of *C. rutilus* tended not to differ significantly among habitat types. With consistency in all habitats, mature *C. rutilus* appeared to be in better condition than immature animals. Mature females in Habitat III were apparently in better condition than those in

Habitat IV. A difference in the abundance and variety of food could provide an explanation for this difference.

Population density (Scheffer, 1955; Kalela, 1957; Christian, 1961; Chitty and Chitty, 1962; Sheppe, 1963; Krebs, 1964; Bergstedt, 1965; Krebs and Myers, 1974) and stress (Scheffer, 1955; Christian, 1971) are other factors that can affect the body weight and consequently the condition (K) of an animal. If the observed weight is less than predicted weight, then K will be <1, and the animal would be considered in poor condition. According to Krebs and Myers (1974), condition was "poor" in increasing populations and "average" to "good" in declining populations of *Microtus ochrogaster*, a species which undergoes cyclic population fluctuations. Since the abundance of *C. rutilus* was greater in Habitats II and III, one could argue that animals in those habitats would be in "poor" condition because of competition for food resources and mates, and increased stress, but such was not the case. In this study, habitat differences did not appear to influence the condition of the animals.

Since it was desirable to determine an index of population abundance before and after breeding, trapping was conducted in the spring and fall. The onset and termination of breeding may vary somewhat from year to year with weather conditions, food supply or other factors (Venables and Venables, 1965). Several studies (Pinter, 1968; Dyke, 1971; Cole and Batzli, 1979; Krohne, 1980; Batzli and Jung, 1981)

have shown that quality of natural foods affects reproduction in voles and lemmings.

The litter size of rodents may be affected by a variety of factors including season of the year, body weight of female, and age and parity of female (Reading, 1966; Krebs and Myers, 1974). The size of litters observed in this study varied with the season and the body weight and age of the female. In the present study, the mean litter size of OW females in the spring was smaller than that found in the fall (Tables 38 and 40) which is contrary to the findings of Koshkina and Korotkov (1975) in the Salair Foothills in Siberia, where OW females produced larger mean litters in May than July. The first litter of the breeding season was conceived during the first two weeks of May (Table 36) when much of the ground was still snow-covered. Consequently, the effective daylength under the snow would have been shorter than the daylength during the period when the last litter was conceived in late July and early August. This may help explain why the initial litters were smaller than subsequent litters.

As was observed by Koshkina and Korotkov (1975), Dickinson (1976) and Fuller (1977b), overwintered females had significantly larger litters than young-of-the-year females. This was probably in part a function of the larger body size of OW females. In those OW females that had two litters during the breeding season (Table 40), the second litter was usually larger than the first, but not

significantly so, even though the mean weight of the females was greater in July and in the fall than in May, over all habitats.

Females in no one particular habitat produced larger litters or more frequent litters and the number of young per 100 trap nights was not significantly different among any of the habitats. Although more litters were produced in Habitats II and III than in the other habitats, that is merely a reflection of the number of breeding females present within those two habitats. When age class II mature females are considered, the reproductive output per female was lower in Habitats II and III than in the other habitats. This could perhaps be due to competition between the older OW females and age class II females for established home ranges as was observed by Kalela (1957) for *Clethrionomys rufocanus*.

Puberty occurs at a very early age in some microtines and the age at puberty in some species has been shown to be influenced by diet, the social environment, photoperiod (Hasler, 1975), and light intensity and wavelength (Evernden and Fuller, 1972). The rate of maturation and degree of participation in breeding of young-of-the-year animals is the most changeable indicator of the intensity of reproduction of *C. rutilus* (Koshkina and Korotkov, 1975). Its variability is closely tied to density of population (Krebs and Myers, 1974; Koshkina and Korotkov, 1975; Fuller, 1979). In years of low individual density of overwintered

females there is a rapid development of young, and their early inclusion into the breeding population. Conversely, in years of maximum initial numbers of overwintered females, maturation of the young is delayed (Koshkina and Korotkov, 1975).

Spring densities were not significantly different over the three years studied, yet the maturation rate of young-of-the-year differed in the two summers studied. This indicates therefore, that maturation was independent of spring density, which is contrary to the findings of Koshkina and Korotkov (1975). Every animal born in early spring matured in the year of its birth independent of spring density; however, a variable proportion of members of later litters matured. In 1979, fewer males than females matured in age class II (13.5% male vs 31.8% female) and in age classes II and III combined (15.8% male vs 60.5% female). These data are consistent with Koshkina and Korotkov's (1975) findings where the maturation of young males was delayed to a greater degree than that of females in populations of increasing density. In 1980 however, a year of greater vole abundance in the fall, a larger proportion of males (38.5%) than females (17.6%) matured in age class II. For age classes II and III combined, males and females matured at roughly equal rates (41.4% male vs 44.4% female). These data are more in line with Fuller's (1979) study of *C. gapperi* in which males matured at a greater rate than females, but contradict the conclusions drawn by Kalela

(1957) for *C. rufocanus* and Koshkina and Korotkov (1975) for *C. rutilus*.

Differences in habitats could explain the differences in the maturation rate of age class II animals because only in Habitats II and III was there a greater proportion of mature males than females in age class II. Increased aggressiveness due to competition for food, nesting sites and mates in those habitats with relatively little debris and vegetation cover (ie. Habitats I, IV and V) could adversely affect gonad activity, inhibiting maturation, as was found by Clarke (1956) in studies of *M. agrestis*. The greater proportion of mature age class II males in Habitats II and III could be because the quality of these two habitats is superior to the others with regard to more resources and more debris cover. In addition, there were very few age class III and OW males alive in Habitats II and III when age class II males became mature and entered the breeding population, thus reducing competitive encounters among the males of these three age classes.

As has been discussed by Pinter (1968), Sealander (1972) and West (1979), the sequence of maturation is consistent with the view that photoperiod is an important regulatory cue for reproduction in *C. rutilus*. Overwintered and early cohort females exposed to increasing and longer daylength enter reproductive condition, whereas late-summer-born females encounter decreasing and shorter daylengths and do not mature sexually. There would be no

habitat differences in this regard as all habitats would be exposed to similar daylength periods.

CONCLUSION

In summary, if the habitats are ranked according to vole demographic variables, Habitats II and III appeared to be the most favourable with reference to both animal abundance and quality. Table 45 outlines those demographic parameters of *C. rutilus* that were significantly different among the habitat types.

Small mammal distributions, particularly those of microtine rodents, have been shown to be closely related to the type and amount of vegetative cover (eg. Eadie, 1953; Mossman, 1955; Hodgson, 1972; Birney *et al.*, 1976). Habitats II and III consisted of the most mature, least disturbed forests in my study area. Miller and Getz (1972; 1973) concluded that the primary factor influencing the local distribution of *Clethrionomys gapperi* was the amount of cover available in the form of fallen trees and logs, brush piles and rocky areas. Protection from predation is assumed to be the primary reason for greater abundance in sites with more cover.

Habitats II and III possessed much debris and the plant species afforded ground cover for the resident voles. Voles may also prefer habitats where free water is available as standing water, or where adequate water can be obtained through food, as this has been shown to be a limiting factor

in *C. gapperi* abundance (Miller and Getz, 1973; Gunderson, 1959). All habitats except Habitat I were known to possess at least some amount of standing water, with Habitats II and III usually possessing more than the remaining habitats.

Snow cover could play an important role in explaining differences in abundances of voles, especially during spring. In upland sites, such as Habitat II, snow lasts longer in the spring than in any other habitat and thus could provide an extended period of protection from predators for the voles while awaiting the growth of new vegetation. If shortage of moisture and cover prevents the establishment of voles in certain areas, one might expect the species to move into sites where snow persists in early spring. Snow could presumably be used as a direct source of moisture and would also afford protection from predation (Miller and Getz, 1972).

Clethrionomy rutilus is a habitat generalist and as others have noted, for *Clethrionomys* spp. in general, preferences, if any, are weakly expressed. Habitats II and III appeared to be the most favourable with reference to both animal abundance and quality, and as such may be selected for by *C. rutilus*. Either survival is greater in these two areas or dispersal into them is greater than into other habitat types.

When ranking the demographic variables of *C. rutilus* to the habitats, a ranking of 1 is best; consequently the best "quality" habitats, with regard to animal demography, are

those with the lowest mean rank. Since Habitats II and III had the lowest mean rank they appeared to be the better quality habitats which was reflected by *C. rutilus* demographic variables.

TABLES

Table 1. Approximate dates of disappearance of snow and first snow on the habitats of the study area.

Event	Habitat				
	I	II	III	IV	V
Last Snow					
1979	May 23	June 10	June 4	June 1	May 25
1980	May 16	June 3	May 26	May 24	May 18
1981	May 23	June 7	June 2	May 31	May 25
First Snow					
1979	Sept 8	Sept 8	Sept 8	Sept 8	Sept 8
1980	Sept 6	Sept 6	Sept 6	Sept 6	Sept 6
Snow-free Days					
1979	109	91	97	99	107
1980	114	96	104	106	112

Table 2. Climatological data for the summer field seasons of 1979 and 1980, including the monthly number of days with rain and sun, and the monthly maximum and minimum temperatures.

Month:	May		June		July		August		September	
Year:	1979	1980	1979	1980	1979	1980	1979	1980	1979	1980
Dates Data Collected:	21-31	3-31	1-30	1-30	1-31	1-31	1-31	1-31	6-21	1-28
Monthly Number of Days with Sunshine	5	21	13	13	19	13	18	13	8	14
Monthly Number of Days with Rain	8	8	19	10	21	17	8	13	4	17
Monthly Mean Maximum Temperature (°C)	15.4	15.0	16.5	21.9	19.0	18.1	20.1	16.5	13.6	8.7
Monthly Mean Minimum Temperature (°C)	1.0	-0.9	3.2	5.1	6.8	6.2	4.5	2.7	2.6	-0.8
Last Day of Frost			11	3						
First Day of Frost							31	20		
Date Snow Free		24	1							
First Day of Snow									8	4

Table 3. Date On Which Snap Traps Were Set.

Habitat	Trapline Number	1979 May	1979 June	1979 Sept	1980 May	1980 Sept	1981 May
1	1	23		7	16	7	23
	2	27		7	16	7	23
	3		12	15	24	15	31
	4		12	15	24	15	31
2	1	25		9	18	9	25
	2	25		9	18	9	25
	3	26		10	19	10	26
	4	26		10	19	10	26
3	1		12	14	23	14	30
	2		1	14	23	14	30
	3		2	13	22	13	29
	4		2	13	22	13	29
4	1		11	11	20	11	27
	2		11	11	20	11	27
	3		11	12	21	12	28
	4		11	12	21	12	28
5	1	21		5	14	5	21
	2	21		5	14	5	21
	3	22		6	15	6	22
	4	22		6	15	6	22

Table 4. Length of live-trapping transects with number of traps per vegetation type.

Transect	Length (m)	# of Traps Per Vegetation Type				
		I	II	III	IV	V
2	3074	33	17	0	43	13
5	2523	28	30	25	4	0
6	2262	46	14	5	4	9
7	2000	46	18	3	2	0
Total		153	79	33	53	22
% of Total		45.0	23.0	10.0	16.0	6.0

Table 5. Area of habitat types and percentage of live-trapping effort by habitat.

	Habitat				
	I	II	III	IV	V
Area (ha)	709.2	416.9	235.2	200.9	145.7
% of Total	40.0	23.5	13.3	11.3	8.2
% of Trapping Effort	44.9	24.7	13.3	11.1	6.0

Table 6. Dates On Which Live-Traps Were Set.

Transect	Rota Number 1	2	3	4	5	6	7
			1979				
2	June 10	July 1	July 22	Aug 12			
5	June 13	July 4	July 25	Aug 15			
6	June 16	July 7	July 28	Aug 18			
7	June 19	July 10	July 31	Aug 21			
			1980				
5	June 9	June 23	July 7	July 21	Aug 4	Aug 19	Sept' 21
6	June 9	July 23	July 7	July 21	Aug 4	Aug 19	Sept' 20

'Snap-traps replaced live-traps.

Table 7. Marked animals removed by snap-trapping the live-trap sites.

	Number of Animals Marked	Number Recovered During Snap-Trapping	Percent Recovered
Females	58	23	39.7
Males	97	45	46.4

Table 8. Summary of the discriminant function analysis[1] showing the significance of the variables chosen and percent variance explained by the functions.

Species	Significance
Pleurozium schreberi	0.0001
Equisetum arvense	0.0000
Gramineae sp.	0.0000
Mitella nuda	0.0000

Function	Percent of Variance	Cumulative Percent
1	83.16	83.16
2	13.64	96.80
3	2.63	99.43
4	0.57	100.00

[1]See methods section for details of discriminant function analysis.

Table 9. Habitat type description for the study area from data from two vegetation plots (a and b) per habitat.

Characteristics	Habitat Type I a	I b	II a	II b	III a	III b	IV a	IV b	V a	V b
Slope Angle ( )°	8	17	10	17	8	5	5	2	6	6
Slope Aspect *	NE	NE	NE	NE	NE	NE	N	N	NE	N
Topographic Position	Slope-Base		Upper-Slope		Mid-Slope		Mid-Slope		Lower-Slope	
MicroRelief (m)	2	10	2	3	0.5	1	0.5	0.5	0.5	1
Drainage Class	Rapid		Well		Fresh		Fresh		Fresh	
Moisture Regime	Xero-Mesic		Mesic		Mesic		Mesic		Hygro-Mesic	
Soil Type	Dry-Sandy Soil		Clay-Sandy Soil		Clayey to Sandy-Clay		Sandy-Clay With Loam Component		Sandy-Clay With Frozen Organics	

*Direction faced by slope.

Table 10. Estimated percent cover[1] of trees observed by habitat type. Range in parentheses.

Species	Habitat Type				
	I	II	III	IV	V
Abies lasiocarpa	1.75 (0.50-3.00)	38.00 (38.00-38.00)	20.00 (20.00-20.00)	3.00 (3.00-3.00)	10.00 (10.00-10.00)
Picea glauca	0.50 (0.50-0.50)	1.75 (0.50-3.00)	10.00 (10.00-10.00)	38.00 (38.00-38.00)	20.00 (20.00-20.00)
Pinus contorta	15.00 (10.00-20.00)	1.50 (0-3.00)	3.00 (3.00-3.00)	0	0.25 (0-0.50)

[1]Estimated from mid-points of cover-classes (see methods).

Table 11. Mean percent cover[1] of shrubs by habitat type from the 1X1 m[2] microplots. Range in parentheses.

Species	Habitat Type I	II	III	IV	V
Immature Tree (<2m)					
Abies lasiocarpa	1.75[1] (0.50-3.00)	5.05 (4.60-5.50)	8.58 (4.55-12.60)	1.15 (0-2.30)	1.30 (0.30-2.30)
Picea glauca	0.05 (0-0.10)	0 (0-0)	0.20 (0-0.40)	3.20 (0.30-6.10)	0.70 (0-1.40)
Pinus contorta	1.00 (0-2.00)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Shrub					
Alnus crispa	0 (0-0)	0.30 (0-0.60)	0.25[1] (0-0.50)	2.00 (0-4.00)	0.33 (0.30-0.35)
Arctostaphylos rubra	0 (0-0)	0 (0-0)	0 (0-0)	9.50 (7.30-11.70)	2.95 (1.35-4.55)
Betula glandulosa	0.53 (0-1.05)	0.15 (0-0.30)	0.03 (0-0.05)	4.15 (1.90-6.40)	1.13 (0.05-2.20)
Empetrum nigrum	21.65 (14.60-28.70)	3.65 (2.85-4.45)	1.38 (0.50-2.25)	4.95 (4.60-5.30)	2.08 (1.50-2.65)

Continued....

Table 11 (Continued)

Species	Habitat Type I	II	III	IV	V
Ledum palustre	2.53 (0.50-4.55)	0.83 (0.35-1.30)	2.28 (1.00-3.55)	3.28 (2.55-4.00)	3.63 (3.45-3.80)
Potentilla fruticosa	0 (0-0)	0 (0-0)	0 (0-0)	3.93 (3.90-3.95)	1.60 (0.35-2.85)
Ribes triste	0 (0-0)	0.05 (0-0.10)	0 (0-0)	0 (0-0)	0 (0-0)
Ribes spp.	0 (0-0)	0 (0-0)	0.15 (0-0.30)	0 (0-0)	0 (0-0)
Rosa acicularis	5.00' (0-10.00)	0 (0-0)	0.28 (0.30-0.25)	1.23 (0.65-1.80)	0.10 (0-0.20)
Salix sp.	0.73 (0.45-1.00)	0.15 (0-0.30)	0.65 (0.30-1.00)	3.80 (2.25-5.35)	5.45 (4.30-6.60)
Vaccinium uliginosum	1.48 (0.10-2.85)	0.03 (0-0.05)	0.98 (0.30-1.65)	2.25 (1.80-2.70)	3.53 (1.05-6.00)
V. vitis - idaea	3.58 (3.45-3.70)	1.08 (0.95-1.20)	2.40 (1.80-3.00)	1.70 (1.45-1.95)	2.08 (1.70-2.45)
Number of Species	10	9	11	12	12
Mean Shrub % Cover	38.30	11.29	17.18	41.14	24.88

'Estimated from mid-points of cover-classes from 10 1X1 m ' microplots per macroplot.

'Present in macroplot (0.1 ha) only.

Table 12. Mean percent cover[1] of herbs by habitat type from the 1X1 m[2] microplots. Range in parentheses.

Herb Species	Habitat Type				
	I	II	III	IV	V
Carex spp.	0 (0-0)	0 (0-0)	0 (0-0)	0.15 (0-0.30)	10.0[2] (10.0-10.0)
Cornus canadensis	0.80 (0.40-1.20)	1.23 (1.20-1.25)	2.25 (2.20-2.30)	1.53 (0.35-2.70)	0.60 (0.40-0.80)
Epilobium angustifolium	0.03 (0-0.05)	0.25[2] (0-0.50)	0 (0-0)	0 (0-0)	0 (0-0)
Equisetum arvense	0 (0-0)	0.38 (0.35-0.40)	0.18 (0-0.35)	0.05 (0.05-0.05)	1.95 (1.75-2.15)
E. silvaticum	0 (0-0)	0.25[2] (0-0.50)	0.20 (0.05-0.35)	0.25 (0.15-0.35)	1.10 (0-2.20)
Geocaulon lividum	0.18 (0-0.35)	0 (0-0)	0 (0-0)	0.30 (0-0.60)	0.15 (0-0.30)
Gramineae spp.	0.03 (0-0.05)	0.05 (0-0.10)	0.65 (0.65-0.65)	0.58 (0.50-0.65)	0.73 (0.65-0.80)
Linnaea borealis	0 (0-0)	0 (0-0)	0 (0-0)	2.10 (1.35-2.85)	2.05 (0-4.10)
Lupinus arcticus	0.53 (0.05-1.00)	0.60 (0.05-1.15)	0 (0-0)	0.05 (0-0.10)	0 (0-0)

Continued.....

Table 12 (Continued)

Herb Species	Habitat Type I	II	III	IV	V
Mertensia paniculata	0 (0-0)	0.03 (0-0.05)	0 (0-0)	0.43 (0.35-0.50)	0.13 (0.05-0.20)
Mitella nuda	0 (0-0)	0.03 (0-0.05)	0 (0-0)	0.98 (0.95-1.00)	0.20 (0.10-0.30)
Orchidaceae sp.	0 (0-0)	0.03 (0-0.05)	0 (0-0)	0 (0-0)	0.03 (0-0.05)
Pedicularis labradorica	0 (0-0)	0 (0-0)	0 (0-0)	0.05 (0-0.10)	0 (0-0)
Petasites sp.	0 (0-0)	0.18 (0-0.35)	0.55 (0.15-0.95)	0.45 (0.30-0.60)	1.03 (0-2.05)
Pyrola spp.	0 (0-0)	0.45 (0.30-0.60)	1.00 (0.30-1.70)	0.48 (0.30-0.65)	0.05 (0-0.10)
Ranunculaceae	0.08 (0-0.15)	0.20 (0.05-0.35)	0 (0-0)	0 (0-0)	0.03 (0-0.05)
Rubus arcticus	0 (0-0)	0.03 (0-0.05)	0.05 (0-0.10)	0.40 (0.20-0.60)	0.28 (0.20-0.35)
R. chamaemorus	0 (0-0)	0 (0-0)	0.65 (0.30-1.00)	0.03 (0-0.05)	1.10 (0.10-2.10)
Viola sp.	0 (0-0)	0.03 (0-0.05)	0 (0-0)	0.03 (0-0.05)	0.03 (0-0.05)

Continued...

Table 12 (Continued)

Herb Species	Habitat Type I	II	III	IV	V
Lycopodium annotinum	0.50 (0-1.00)	0.15 (0-0.30)	2.15 (1.70-2.60)	0 (0-0)	0 (0-0)
L. complanatum	0.50 (0-1.00)	0.15 (0-0.30)	0 (0-0)	0 (0-0)	0.15 (0-0.30)
Moneses uniflora	0 (0-0)	0.50' (0.50-0.50)	1.50' (0-3.00)	0.25' (0-0.50)	0 (0-0)
Senecio triangularis	0 (0-0)	0 (0-0)	0 (0-0)	0.25' (0-0.50)	0 (0-0)
Number of Species	8	17	10	18	16
Mean Herb % Cover	2.65	3.54	7.68	7.86	9.61

'Estimated from mid-points of cover-classes from 10 1X1 m' microplots per macroplots.

'Present in macroplot (0.1 ha) only.

Table 13. Mean percent cover[1] of mosses and lichens by habitat type from the 1X1 m² microplots. Range in parentheses.

Moss and Lichen Species	Habitat Type I	II	III	IV	V
Cladonia sp.	3.05 (0.55-5.55)	4.43 (3.85-5.00)	0.73 (0.10-1.35)	0.15 (0-0.30)	0.18 (0.05-0.30)
Cladina stellaris	0.30 (0-0.60)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
C. mitis	5.30 (0.80-9.80)	11.98 (7.70-16.25)	1.35 (0.05-2.65)	1.18 (0.35-2.00)	0.68 (0.30-1.05)
C. rangiferina	2.15 (0-4.30)	0.75 (0.60-0.90)	0.15 (0-0.30)	0.18 (0.05-0.30)	0.68 (0.05-1.30)
Stereocaulon sp.	0.05 (0.05-0.05)	0.03 (0-0.05)	0.15 (0-0.30)	0 (0-0)	0 (0-0)
Peltigera aphthosa	8.55 (5.80-11.30)	7.70 (5.95-9.45)	4.05 (3.85-4.25)	0.80 (0.65-0.95)	0.45 0.35-0.55)
Nephroma arcticum	0.50 (0-1.00)	1.15 (0.30-2.00)	1.98 (1.00-2.95)	1.75' (0.50-3.00)	0.25' (0-0.50)
Mesophytic mosses	5.68 (0.45-10.90)	5.76 (2.57-8.95)	12.38 (0.75-24.00)	2.60 (0-5.20)	11.33 (4.65-18.00)

Continued.....

Table 13 (Continued)

Moss and Lichen Species	Habitat Type I	II	III	IV	V
Pleurozium schreberi	1.53 (0.65-2.40)	41.90 (30.80-53.00)	60.75 (52.10-69.40)	71.00 (63.50-78.50)	51.10 (48.00-54.20)
Sphagnum sp.	0 (0-0)	0 (0-0)	9.50 (0-19.00)	0 (0-0)	10.00[1] (10.00-10.00)
Mean Lichen % Cover	19.90	26.04	8.41	2.31	1.99
Mean Bryophyte % Cover	7.21	47.66	82.63	73.60	62.43

[1]Estimated from mid-points of cover-classes from 10 1X1 m² microplots per macroplot.

[2]Present in macroplot (0.1 ha) only.

Table 14. Number of individuals, number of species, diversity, and evenness of species captured in the spring trapping sessions.

Year	Habitat I	II	III	IV	V	Total
			Number in Sample (N)			
1979	8	17	14	8	16	63
1980	3	11	12	9	7	42
1981	4	12	10	10	12	48
			Number of Species (S)			
1979	1	2	2	3	5	5
1980	1	2	3	2	2	5
1981	2	2	3	2	4	6
			Diversity (H)			
1979	0	0.67	0.37	1.06	1.72	1.11
1980	0	0.44	1.19	0.50	0.59	0.96
1981	0.81	0.41	0.92	0.47	1.55	1.21
			Evenness (J)			
1979	0	0.67	0.37	0.67	0.74	0.48
1980	0	0.44	0.75	0.50	0.59	0.41
1981	0.81	0.41	0.58	0.47	0.78	0.47

Table 15. Number of individuals, number of species, diversity, and evenness of species captured in the fall trapping sessions.

Year	Habitat I	II	III	IV	V	Total
			Number in Sample (N)			
1979	25	61	58	25	46	215
1980	44	84	70	42	67	307
			Number of Species (S)			
1979	4	4	3	3	6	7
1980	3	4	5	4	6	8
			Diversity (H)			
1979	1.03	0.45	0.34	0.79	1.36	0.92
1980	0.67	0.35	0.51	0.77	1.22	0.78
			Evenness (J)			
1979	0.51	0.22	0.22	0.50	0.53	0.33
1980	0.33	0.17	0.22	0.39	0.44	0.26

Table 16. Species diversity (H) and evenness (J) of small mammals captured in the study area during spring trapping; 1979, 1980 and 1981 combined.

Species	Habitat					
	I	II	III	IV	V	Total
C. rutilus	14	35	29	23	22	123
L. sibiricus	0	5	0	0	2	7
M. pennsylvanicus	0	0	1	2	5	8
M. longicaudus	1	0	0	0	0	1
P. intermedius	0	0	4	1	4	9
S. borealis	0	0	1	0	2	3
Sorex cinereus	0	0	1	1	0	2
# of Individuals	15	40	36	27	35	153
# of Species	2	2	5	4	5	7
H (Diversity)	0.35	0.54	1.03	0.83	1.65	1.16
J (Evenness)	0.35	0.54	0.45	0.41	0.71	0.41

Table 17. Species diversity (H) and evenness (J) of small mammals captured in the study area during fall trapping, 1979 and 1980 combined.

Species	Habitat					
	I	II	III	IV	V	Total
C. rutilus	59	137	120	57	83	456
L. sibiricus	0	3	4	0	2	9
M. pennsylvanicus	0	2	1	6	19	28
M. longicaudus	0	0	0	1	0	1
P. intermedius	3	1	0	0	2	6
S. borealis	0	0	1	0	3	4
Sorex cinereus	5	1	2	0	2	10
S. obscurus	2	1	0	3	2	8
# of Individuals	69	145	128	67	113	522
# of Species	4	6	5	4	7	8
H (Diversity)	0.81	0.43	0.45	0.80	1.31	0.84
J (Evenness)	0.41	0.17	0.19	0.40	0.47	0.28

Table 18. The degree of difference (Dd and rD) between habitat types during spring trapping (1979, 1980 and 1981 combined).

Species	Numbers Captured in Habitat Pairs									
	I&II	I&III	I&IV	I&V	II&III	II&IV	II&V	III&IV	III&V	IV&V
C. rutilis	49	43	37	36	64	58	57	52	51	45
L. sibiricus	5	0	0	2	5	5	7	0	2	2
M. pennsylvanicus	0	1	2	5	1	2	5	3	6	7
M. longicaudus	1	1	1	1	0	0	0	0	0	0
P. intermedius	0	4	1	4	4	1	4	5	8	5
S. borealis	0	1	0	2	1	0	2	1	3	2
Sorex cinereus	0	1	1	0	1	1	0	2	1	1
Total Individuals	55	51	42	50	76	67	75	63	71	62
Total Species	3	6	5	6	6	5	5	5	6	6
H (Diversity)	0.57	0.94	0.76	1.45	0.94	0.79	1.25	0.98	1.42	1.40
J (Evenness)	0.36	0.36	0.33	0.56	0.36	0.34	0.54	0.42	0.55	0.54
Dd (DIVdiff)	0.12	0.25	0.17	0.45	0.15	0.11	0.15	0.05	0.08	0.16
rD (Relative DIVdiff)	8.64	18.64	12.12	36.30	10.83	7.65	10.81	3.51	5.74	11.72

Table 19. The degree of difference (Dd and rD) between habitat types during fall trapping (1979 and 1980 combined).

Species	Numbers Captured in Habitat Pairs									
	I&II	I&III	I&IV	I&V	II&III	II&IV	II&V	III&IV	III&V	IV&V
C. rutilis	196	179	116	142	257	194	220	177	203	140
L. sibiricus	3	4	0	2	7	3	5	4	6	2
M. pennsylvanicus	2	1	6	19	3	8	21	7	20	25
M. longicaudus	0	0	1	0	0	1	0	1	0	1
P. intermedius	4	3	3	5	1	1	3	0	2	2
S. borealis	0	1	0	3	1	0	3	1	4	3
Sorex cinereus	6	7	5	7	3	1	3	2	4	2
S. obscurus	3	2	5	4	1	4	3	3	2	5
Total Individuals	214	197	136	182	273	212	258	195	241	180
Total Species	6	7	6	7	7	7	7	7	7	8
H (Diversity)	0.60	0.65	0.92	1.23	0.45	0.60	0.90	0.65	0.95	1.18
J (Evenness)	0.23	0.23	0.36	0.44	0.16	0.21	0.32	0.23	0.34	0.39
Dd (DIVdiff)	0	0.02	0.11	0.17	0.01	0	0.03	0.03	0.07	0.12
rD (Relative DIVdiff)	0	1.25	8.03	12.64	0.89	0	2.17	2.00	5.09	8.80

Table 20. rD values and percentage of total rD attributed to various pairs of habitats.

	Spring (Years Combined)			Fall (Years Combined)		
Habitats	Rank	rD	%	Rank	rD	%
I-V	1	36.30	28.8	1	12.64	30.9
I-III	2	18.64	14.8	7	1.25	3.1
I-IV	3	12.12	9.6	3	8.03	19.6
IV-V	4	11.72	9.3	2	8.80	21.5
II-III	5	10.83	8.6	8	0.89	2.2
II-V	6	10.81	8.6	5	2.17	5.3
I-II	7	8.64	6.9	9.5	0	0
II-IV	8	7.65	6.1	9.5	0	0
III-V	9	5.74	4.6	4	5.09	12.5
III-IV	10	3.51	2.8	6	2.00	4.9
Σ		125.96			40.87	
$\bar{X}$		12.60			4.09	
Sx.		9.28			4.37	
S.E.		2.94			1.38	

Table 21. Results of the Student-Newman-Keuls Procedure for the fall (1979, 1980) mean captures per trapline of *C. rutilus*. Sexes combined.

A) All Ages Combined

Habitat	IV	I	V	III	II
Mean Capture	7.13	7.38	10.38	15.00	17.13

B) Age Class II

Habitat	IV	I	V	III	II
Mean Capture	2.00	3.00	4.75	6.25	7.13

C) Age Class III

Habitat	I	V	IV	II	III
Mean Capture	0.25	0.63	1.25	1.25	1.63

D) Age Classes II & III Combined

Habitat	I	IV	V	III	II
Mean Capture	3.25	3.25	5.38	7.88	8.38

Table 22. Results of the Student-Newman-Keuls Procedure for the fall (1979, 1980) mean captures of *C. rutilus* males in 150 T.N.

A) All Ages Combined

Habitat	IV	I	V	III	II
Mean Capture	3.63	4.50	4.75	8.13	9.13

B) Age Class II

Habitat	IV	I	V	III	II
Mean Capture	1.50	2.00	2.63	4.50	4.50

C) Age Classes II & III Combined

Habitat	IV	I	V	II	III
Mean Capture	1.63	2.13	2.63	4.63	4.88

Table 23. Results of the Student-Newman-Keuls Procedure for the fall (1979, 1980) mean captures of *C. rutilus* females in 150 T.N.

A) All Ages Combined

Habitat	I	IV	V	III	II
Mean Capture	2.88	3.50	5.63	6.88	8.00

B) Age Class II

Habitat	IV	I	III	V	II
Mean Capture	0.50	1.00	1.75	2.13	2.63

C) Age Classes II & III Combined

Habitat	I	IV	V	III	II
Mean Capture	1.13	1.63	2.75	3.00	3.75

Table 24. Results of the Student-Newman-Keuls Procedure for the fall (1979 and 1980) mean trapline captures of *C. rutilus*. All age classes combined (F=female, M=male).

I-F	IV-F	IV-M	I-M	V-M	V-F	III-F	II-F	III-M	II-M
2.88	3.50	3.63	4.50	4.75	5.63	6.88	8.00	8.13	9.13

Table 25. Proportion of males caught in the fall trapping sessions. Sample sizes in parentheses and degrees of freedom in brackets.

Age Class	Year	Habitats I	II	III	IV	V	Pooled	G-Statistics (Habitats Combined) Gh	Gp	Gt
I	1979	0.69(13)	0.53(32)	0.50(28)	0.70(10)	0.47(17)	0.55(100)	1.56[4]	0.64[1]	2.20[5]
	1980	0.47(17)	0.50(24)	0.40(25)	0.44(16)	0.33(18)	0.43(100)	1.11[4]	1.00[1]	2.11[5]
II	1979	0.50(6)	0.59(17)	0.80(20)[1]	0.80(5)	0.36(11)	0.63(59)	4.94[4]	2.89[1]	7.82[5]
	1980	0.72(18)	0.65(40)	0.67(30)	0.73(11)	0.63(27)	0.67(126)	0.41[4]	11.03[1][3]	11.44[5][3]
III	1979	(0)	0.00(3)	0.14(7)	0.00(4)	0.00(3)	0.06(17)	0.15[3]	7.72[1][2]	7.87[4]
	1980	0.50(2)	0.14(7)	0.33(6)	0.17(6)	0.00(2)	0.22(23)	1.07[4]	3.62[1]	4.69[5]
IV(OW)	1979	1.00(1)	0.25(4)	(0)	0.50(2)	(0)	0.43(7)	0.11[2]	0.14[1]	0.25[3]
	1980	0.50(2)	0.56(9)	0.50(4)	0.33(3)	0.60(5)	0.52(23)	0.00[4]	0.00[1]	0.00[5]
II&III	1979	0.50(6)	0.50(20)	0.63(27)	0.44(9)	0.29(14)	0.50(76)	3.16[4]	0.01[1]	3.17[5]
	1980	0.70(20)	0.57(47)	0.61(36)	0.53(17)	0.59(29)	0.60(149)	1.31[4]	3.88[1][3]	5.19[5]

[1] $P<0.05$

[2] $P<0.01$

[3] $P<0.005$

Table 26. Proportion (P) of age classes of fall captured *C. rutilus* (sexes combined). 1980 values are drawn from snap-trapping of habitats and live-trap lines.

	Age Category										
	I		II		III		IV		II & III		
Year	N	P	N	P	N	P	N	P	N	P	Total
1979	100	.55	59	.32	17	.09	7	.04	76	.42	183
1980	173	.34	247	.48	50	.10	40	.08	297	.58	510
Probability[1]	$9.4X10^{-1}$		$9.8X10^{-1}$		0.23		0.05		0.0001		

[1]Fisher's Exact Test

Table 27. Proportion of age class n in samples of *C. rutilus* in fall snap-trapping. 1980 data includes snap-trapping of habitats and live-trap lines. Sexes are combined. N.S. = not significantly different.

Age Class	Year	Habitat I	II	III	IV	V	Total
I-(Not I)	1979	0.65	0.57	0.51	0.48	0.55	100
	1980	0.43	0.25	0.34	0.43	0.33	173
	G	3.39	18.21	4.46	0.15	4.24	
	P	N.S.	<0.005	<0.05	N.S.	<0.05	
II-(Not II)	1979	0.30	0.30	0.36	0.24	0.35	59
	1980	0.45	0.52	0.49	0.34	0.55	247
	G	1.53	8.28	2.31	0.73	3.34	
	P	N.S.	<0.005	N.S.	N.S.	N.S.	
III-(Not III)	1979	0	0.05	0.13	0.19	0.10	17
	1980	0.08	0.12	0.10	0.15	0.04	50
	G		2.44	0.38	0.18	0.93	
	P	0.24[1]	N.S.	N.S.	N.S.	N.S.	
IV-(Not IV)	1979	0.05	0.07	0	0.10	0	7
	1980	0.05	0.10	0.08	0.09	0.07	50
	G	6X10	0.39		0.02		
	P	N.S.	N.S.	0.001[1]	N.S.	0.14[1]	
II+III-(Not II+III)	1979	0.30	0.36	0.49	0.43	0.45	76
	1980	0.52	0.65	0.58	0.49	0.60	297
	G	3.44	14.36	1.26	0.22	1.81	
	P	N.S.	<0.005	N.S.	N.S.	N.S.	

[1]Values of P determined by Fisher's Exact Test.

Table 28. The Student-Newman-Keuls Procedure for the fall (1979,1980) biomass of *C. rutilus*, in 1200 T.N. following a one-way analysis of variance.

A) Sexes Combined

Habitat	I	IV	V	III	II
Mean Biomass	73.40	74.13	106.44	149.88	178.88

B) Males

Habitat	IV	I	V	III	II
Mean Biomass	70.54	87.93	95.54	157.30	182.19

C) Females

Habitat	I	IV	V	III	II
Mean Biomass	58.88	77.71	117.34	142.45	175.58

Table 29. The Student-Newman-Keuls Procedure for the spring body length of *C. rutilus*, in 1200 T.N. following an analysis of covariance.

1979

Habitat	V	I	II	III	IV
Mean Body Length	101.56	102.13	104.14	105.08	106.20

1980

Habitat	IV	V	I	III	II
Mean Body Length	94.50	98.67	101.67	102.38	103.50

1981

Habitat	I	V	IV	III	II
Mean Body Length	98.67	99.86	101.22	102.63	102.64

Table 30. Mean (± S.E.) body lengths of the combined 1979 and 1980 fall sample of the late cohort *C. rutilus*. Sample size in parentheses.

A) Years Separate - Sexes Combined

	Habitat				
Year	I	II	III	IV	V
1979	86.54±1.82 (13)	87.00±0.79 (32)	88.43±0.96 (28)	87.10±2.41 (10)	89.65±0.95 (17)
1980	90.71±0.87 (17)	87.58±1.03 (24)	85.80±1.44 (25)	86.19±1.05 (16)	84.50±1.32 (18)

F(1,190)(Year)=0.96 N.S.

F(4,190)(Habitat)=0.57 N.S.

B) Years Combined - Sexes Separate

	Habitat				
Sex	I	II	III	IV	V
Males	90.12±1.32 (17)	87.90±0.97 (29)	87.54±1.50 (24)	85.50±1.64 (14)	87.43±1.93 (14)
Females	87.31±1.43 (13)	86.56±0.78 (27)	86.90±0.98 (29)	87.75±1.43 (12)	86.71±0.89 (21)

F(1,190)(Sex)=0.63 N.S.

F(4,190)(Habitat)=0.60 N.S.

Table 31. Mean body length (± S.E.) of immature (I) and mature (M) early cohort *C. rutilus* captured in the fall 1979 and 1980 trapping sessions. Sample size in parentheses.

Sex	Repro. Status	Habitat				
		I	II	III	IV	V
Male	I	91.47±0.58 (15)	91.96±0.76 (24)	93.67±0.49 (27)	94.00±1.00 (9)	93.50±0.75 (14)
	M	97.00±2.00 (2)	93.69±0.91 (13)	94.58±0.96 (12)	94.50±1.32 (4)	94.86±1.22 (7)
Female	I	93.67±1.43 (6)	92.18±1.32 (17)	91.50±0.80 (12)	92.00±2.00 (3)	89.50±0.82 (10)
	M	99.00±0.00 (3)	103.15±1.54 (13)	105.08±0.98 (12)	104.20±1.03 (10)	103.83±1.36 (12)

Table 32. Mean condition factor (± S.E.) for the combined 1979 and 1980 fall sample of the late cohort *C. rutilus*. Sample size in parentheses.

Year	Habitat I	II	III	IV	V
MALES					
1979	0.901±0.040 (9)	0.880±0.032 (17)	0.855±0.036 (14)	0.864±0.061 (7)	0.939±0.034 (8)
1980	0.949±0.035 (8)	0.881±0.030 (12)	0.866±0.055 (10)	0.881±0.035 (7)	0.800±0.061 (6)
	F(1,88) Year = 0.19 N.S. F(4,88) Habitat = 0.67 N.S.				
FEMALES					
1979	0.978±0.181 (4)	0.858±0.031 (15)	0.886±0.029 (13)	0.919±0.008 (3)	0.880±0.026 (8)
1980	0.886±0.015 (9)	0.880±0.036 (12)	0.859±0.032 (15)	0.860±0.034 (9)	0.811±0.038 (12)
	F(1,90) Year = 2.46 N.S. F(4,90) Habitat = 0.87 N.S.				

Table 33. Mean condition factor (± S.E.) for the combined 1979 and 1980 fall sample of the early cohort male *C. rutilus*. Sample size in parentheses.

	Habitat				
	I	II	III	IV	V
Mature	1.18±0.03 (2)	1.07±0.02 (13)	1.10±0.02 (12)	1.04±0.03 (4)	1.06±0.03 (7)
Immature	0.98±0.02 (15)	1.01±0.02 (24)	1.02±0.02 (26)	0.99±0.05 (9)	1.02±0.01 (14)

F(1,116) (Maturity) = 14.72 P<0.001
F(4,116) (Habitat) = 0.90 N.S.

Table 34. Mean condition factor (± S.E.) for the combined 1979 and 1980 fall sample of the early cohort female *C. rutilus*. Sample size in parentheses.

	Habitat				
	I	II	III	IV	V
Mature	1.35±0.01 (3)	1.31±0.04 (13)	1.43±0.04 (12)	1.27±0.04 (10)	1.34±0.04 (12)
Immature	1.07±0.10 (6)	1.02±0.03 (16)	1.00±0.02 (12)	0.85±0.05 (3)	0.97±0.02 (10)

F(1,87) (Maturity) = 139.87 P<0.001
F(4,87) (Habitat) = 2.76 P<0.05

Table 35. The Student-Newman-Keuls Procedure for the mean condition factor value of mature (m) and immmature (i) early cohort female *C. rutilus*, in 1200 T.N. following a two-way analysis of variance. Roman numerals for habitats.

IV (i)	V (i)	III (i)	II (i)	I (i)	IV (m)	II (m)	V (m)	I (m)	III (m)
0.85	0.97	1.00	1.02	1.07	1.27	1.31	1.34	1.35	1.43

Table 36. Dates of reproductive activities of female *C. rutilus* calculated by back-dating, based on a gestation period of 17 days.

	Habitat				
	I	II	III	IV	V
Earliest Pregnancy					
1979	May 7-8	May 9	May 13	May 13-15	-
1980	-	May 3-4	May 9	May 6	May 7
1981	-	May 12	May 13	May 13-14	May 10-12
Last Pregnancy					
1979	-	Sept 12	-	Sept 15	Sept 7
1980	Sept 8	-	-	-	-

Table 37. Pregnancy rates in the fall 1979 and 1980 combined sample of *C. rutilus*. Includes those animals captured in snap-trapping of habitats and snap-trapping of live-trap lines.

Reproductive Condition and Age Class	Habitat				
	I	II	III	IV	V
Number in Sample:					
Age Class II	21	36	21	7	22
Age Class III	8	20	14	9	6
Age Class IV(OW)	4	10	4	4	2
% of Females With 1 Litter:					
Age Class II	14.3	8.3	14.3	14.3	27.3
Age Class III	37.5	45.0	42.9	77.8	33.3
Age Class IV(OW)	0.0	40.0	0.0	0.0	50.0
% of Females With 2 Litters:					
Age Class II	4.8	2.8	0.0	14.3	13.6
Age Class III	62.5	55.0	57.1	22.2	66.7
Age Class IV(OW)	100.0	60.0	100.0	100.0	50.0
% of Immature Females:					
Age Class II	80.9	88.9	85.7	71.4	59.1
Age Class III	0.0	0.0	0.0	0.0	0.0
Age Class IV(OW)	0.0	0.0	0.0	0.0	0.0

Table 38. Mean litter size (± standard error) of OW *C. rutilus* in spring-trapping 1979, 1980 and 1981. Litter sample size in parentheses.

	Habitat					
Year	I	II	III	IV	V	Total
1979	4.67±0.33(3)	3.50±0.43(6)	4.44±0.24(9)	4.50±2.50(2)	0 (0)	4.20±0.27(21)
1980	0 (0)	4.33±0.67(3)	4.33±0.67(3)	4.25±0.63(4)	4.00±0.00(1)	4.27±0.30(11)
1981	0 (0)	4.67±0.33(3)	4.00±0.00(3)	5.00±1.15(3)	3.75±0.25(4)	4.31±0.29(13)
Total	4.67±0.33(3)	4.00±0.30(12)	4.33±0.19(15)	4.56±0.60(9)	3.80±0.20(5)	4.28±0.16(45)

Table 39. The Student-Newman-Keuls Procedure for the mean number of embryos in the last litter of age class III *C. rutilus*, following a one-way analysis of variance. Fall 1979 and 1980 Combined.

	Habitat				
	I	V	II	III	IV
Mean Number of Embryos in Last Litter	4.63	5.83	6.09	6.64	7.67

Table 40. Mean litter size (± S.E.), mean number of litters and output per female and per 100 T.N. of *C. rutilus* captured in the combined 1979 and 1980 fall trapping sessions, by habitat and age. Sample size in parentheses.

	Habitat					
	I	II	III	IV	V	All
Age Class II						
One Litter	4.33±0.33(3)	6.00±1.73(3)	3.33±1.20(3)	10.00 (1)	7.00±0.86(6)	5.81±0.65(16)
Two Litters	7.00 (1)	4.00 (1)	(0)	5.00 (1)	6.67±0.88(3)	6.00±0.63(6)
Mean No. Litters	1.25	1.25	1.00	1.50	1.33	1.27
Mean Litter Size	5.00	5.50	3.33	7.50	6.89	5.86
Embryos/Breeding Female	6.25	6.88	3.33	11.25	9.16	7.44
% Females Breeding	19.0	11.1	14.3	28.6	40.9	20.6
Output/Female	1.19	0.76	0.47	3.22	3.76	1.53
Output/100 T.N.	0.79	0.51	0.24	1.07	5.64	5.61

Continued.....

Table 40 (Continued)

	Habitat					
	I	II	III	IV	V	All
Age Class III						
One Litter	2.33±0.88(3)	6.44±0.82(9)	6.00±0.82(6)	8.00±0.87(7)	5.00±1.00(2)	6.19±0.50(27)
Two Litters	6.00±0.65(5)	5.91±0.65(11)	7.13±0.48(8)	6.50±0.50(2)	6.25±0.95(4)	6.33±0.32(30)
Mean No. Litters	1.63	1.55	1.57	1.22	1.67	1.53
Mean Litter Size	4.62	6.15	6.65	7.67	5.83	6.26
Embryos/Breeding Female	7.53	9.53	10.44	9.36	9.74	9.58
% Females Breeding	100.0	100.0	100.0	100.0	100.0	100.0
Output/Female	7.53	9.53	10.44	9.36	9.74	9.58
Output/[illegible]T.N.	10.04	31.77	24.36	14.04	9.74	91.01

Continued.....

Table 40 (Continued)

	Habitat					
	I	II	III	IV	V	All
Age Class OW						
One Litter	(0)	7.75±1.31(4)	(0)	(0)	9.00 (1)	8.00±1.05(5)
Two Litters	9.00±0.41(4)	10.00±1.13(6)	8.25±0.85(4)	6.75±0.95(4)	7.00 (1)	8.58±0.51(19)
Mean No. Litters	2.00	1.60	2.00	2.00	1.50	1.79
Mean Litter Size	9.00	9.10	8.25	6.75	8.00	8.46
Embryos/Breeding Female	18.00	14.56	16.50	13.50	12.00	15.14
% Females Breeding	100.0	100.0	100.0	100.0	100.0	100.0
Output/Female	18.00	14.56	16.50	13.50	12.00	15.14
Output/100 T.N.	12.00	24.27	11.00	9.00	4.00	60.56

Table 41. Weighted average output of embryos per female in the combined 1979 and 1980 fall sample, by habitat and age.

Age Class	Habitat				
	I	II	III	IV	V
II	0.76	0.42	0.25	1.13	2.74
III	1.81	2.86	3.76	4.21	1.95
OW	2.16	2.18	1.65	2.70	0.84
Total	4.73	5.46	5.66	8.04	5.53

Table 42. Proportion of mature males by age class.

Season	Age Class	Habitat I %	I N	II %	II N	III %	III N	IV %	IV N	V %	V N	Total %	Total N
Spring:													
May	OW	100	8	100	22	100	14	100	12	100	15	100	71
Summer:													
June	OW	100	1		0	100	3	100	3		0	100	7
July	I		0	0	1	80	5	100	6	100	2	86	14
	II		0	100	2		0	100	2		0	100	4
	OW		0	100	2	100	6	100	3	100	3	100	14
Aug.	II	83	6	54	13[1]		0		0	100	2	67	21
Fall:													
Sept	I	5	38	0	37	0	29	0	18	0	17	1.4	139
	II	15	39	36	66	45	53	29	14	35	26	34	198
	III	100	1	100	2	100	4	100	2		0	100	9
	OW	100	3	100	10	100	5	100	2	100	3	100	23

[1]Includes a mature age class III individual.

Table 43. Summary of *C. rutilus* live-trapping results from 1979 and 1980.

		1979		1980		Total		Total		/100 T.N.	
Habitat	Number of Traps	Number Marked	Total Captures	Number Marked	Total Captures	Number Marked	Total Captures	Individuals /Trap	Captures /Trap	Number Marked	Total Captures
I	153(45.0%)	23	39	57	120	80	159	0.52	1.04	2.84	5.02
II	79(23.2%)	13	30	61	137	74	167	0.94	2.11	5.00	9.60
III	33(9.7%)	5	6	44	133	49	139	1.49	4.21	5.77	14.85
IV	53(15.6%)	8	10	9	32	17	42	0.32	0.79	2.44	5.38
V	22(6.5%)	1	2	5	8	6	10	0.27	0.45	1.64	2.35
Total	340(100%)	50	87	176	430	226	517	0.66	1.52		

Table 44. Proportion of males, by age class of *C. rutilus* removed from the live-trap lines during the seventh rota, 1980. Sample size, male and female combined, in parentheses.

Habitat	Age Categories			
	I	II	III	IV
I	0.60 (35)	0.63 (35)	0.00 (7)	0.25 (4)
II	0.47 (17)	0.66 (44)	0.08 (12)	0.57 (7)
III	0.36 (14)	0.73 (26)	0.25 (5)	0.60 (5)
IV	1.00 (4)	0.40 (5)	1.00 (1)	0.00 (1)
V	0.75 (4)	0.50 (10)	0.00 (1)	0.00 (0)
Total	0.56 (73)	0.64 (120)	0.12 (26)	0.47 (17)
Gp	0.86	9.77'	17.40'	0.06

'$P<0.005$

Table 45. Habitat ranking with regard to those demographic variables of *C. rutilus* significantly different among habitats.

C. rutilus Characteristic	Habitat I	II	III	IV	V
Abundance	4	1	2	5	3
Biomass					
Spring	5	1	2	3	4
Fall	5	1	2	4	3
Body Lengths					
Spring 1979	4	3	2	1	5
Spring 1980	3	1	2	5	4
Spring 1981	5	1	2	3	4
Maturity of Age Class II					
Males	5	2	1	4	3
Females	3	5	4	2	1
Reproductive Output					
# of Embryos/Female	2	5	1	3	4
Output/100 T.N.	5	1	2	4	3
Mean Rank	4.1	2.1	2.0	3.4	3.4

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APPENDICES

Appendix 1. Standard vegetation survey form for vegetation plot 1, Habitat 1.

BOREAL PLANT COMMUNITY CLASSIFICATION PROJECT
PLANT ECOLOGY SECTION, BOTANY DEPARTMENT,
UNIVERSITY OF ALBERTA

RELEVÉ No. 1-1 DATE JULY 6/80 OBSERVERS S.S.B. & M.R.

FORMATION Name

UNESCO Code IBP Code

SOCIATION Name

LOCATION HABITAT 1 BETWEEN TRAPLINES 1 & 2
OFF ROAD BETWEEN TRANSECTS 1 & 2

LEGAL STATUS

AIRPHOTO Date Scale Number

MAP Date Scale Name

Lat. ° ' N Long. ° ' W Elev. m ft ASL

SITE Land Type MAINLY FLAT AND DRY

Land Form BETWEEN ROAD AND EVELYN CREEK

Plot Area 0.1 ha | Shape 20 x 50 m | Slope 8 ° | Aspect N.E. 48°

Topographic Position SLOPE - BASE Microrelief 2.0 m

SOIL Order Great Group

Drainage Class	Moisture Regime	Ground Cover	Stability Index
1 v. rapid	1 xeric	bare rock 0%	1 unstable
(2) rapid	(2) xero-mesic	min. soil 5 %	2 rapid change
3 well	3 mesic	humus 10 %	(3) moderate chg
4 fresh	4 hygro-mesic	wood 10 %	4 slow change
5 impeded	5 hygric	water 0 %	5 stable
6 poor	6 hygro-hydric	gym detr 20 % (CONIFEROUS)	6 climax
7 stagnant	7 hydric	ang detr 5 %	bryoid 50 % (MOSS+LICHEN)

HABITAT Description IMMATURE Pinus contorta DOMINATED FOREST FAIRLY OPEN WITH Equisetum arvense AND Ledum palustre. TREES MORE DENSE BUT SMALLER THAN VEG-PLOT 1-2.

HISTORY AND SUCCESSIONAL STATUS FAIRLY RECENT BURN, LESS THAN 95 YEARS AGO.

Humus thickness 6.0 cm. texture UNDEVELOPED pH=

Top20 cm mineral stone vol 5-10 %, texture CLAY, SMALL ROCKS pH=

PHOTOGRAPHY No. Slides Conditions

1 PLOT1 PHOTO1	2 PLOT 2 PHOTO 2	3 PLOT 3 PHOTO 3	4 PLOT 4 PHOTO 4	
5 " 5 " 5	6 " 6 " 6	7 " 7 " 7	8 " 8 " 8	
9 " 9 " 9	10 " 10 " 10	11	12	

GENERAL PLOT PHOTOS 11-19
SOIL PIT PHOTO 20

BOREAL PLANT COMMUNITY CLASSIFICATION PROJECT
PLANT ECOLOGY SECTION, BOTANY DEPARTMENT
UNIVERSITY OF ALBERTA

RELEVÉ No.	DATE JULY 6/80		PHYSIOGNOMIC DATA							
GROWTH-FORMS	dbh ( )		Ht($\bar{X}$)	CC	Ht($\bar{X}$)	CC	Ht($\bar{X}$)	CC	Tot CC	
Trees	max	$\bar{X}$	2-10m		10-20		>20m			
1.Broadlf dec	-	-	-	-	-	-	-	-	-	
2.Needlelf dec	-	-	-	-	-	-	-	-	-	
3.Needlelf evg	14	6	8	3	-	-	-	-	3	PICO, PIGL
Shrubs (+ juvenile trees)			0-0.3m		0.3-2m		>2m			
4.Broadleaf deciduous			0.28	2	1.7	+	3.0	+	2	BEGL, VAUL, ALCR; SALIX, ROAC.
5.Broadleaf evergreen			10 cm	1	0.5	2	-	-	2	LEPA, VAVI.
6.Needleleaf deciduous			-	-	-	-	-	-	-	
7.Needleleaf evergreen			10 cm	4	2	1	-	-	4	ABLA, PICO, PIGL, EMNI.
Herbs			0-10cm		10-30		30cm			
8.Compoundleaf forbs			-		16cm	1	-	-	1	LUAR.
9.Simpleleaf forbs			5 cm	+	12 cm	1	30cm	+	2	COCA, GELI, EPAN, DELPHINEUM
10.Evergreen forbs			-	-	-	-	-	-	-	
11.Graminoids			-	-	30cm	+	-	-	+	
12.Pteridophytes			6cm	+	-	-	-	-	+	LYCO

	cc
Bryoids:Terrestr tot	4
13.Upland bryophytes	1
14.Peatmosses	0
15.Brownmosses	0
16.Fruticose lichens	2
17.Other lichens	3

Size-Age Rel'ns (tree dbh; shrub base)

Species	Diam	Ht(m)	Rings

CLMI, CL sp.
PELTIGERA

Epiphytes:nil=12345=hi

18.Vasculars		on	
19.Bryophytes		on	
20.Lichens	1	on PICO	Alectoria jubata

STRATUM NAME	TREES H	TREES M	TREES L	SHRUBS H	SHRUBS M	SHRUBS L	HERBS H	HERBS M	HERBS L	BRYOPHYTES
Cover % (not CC)	25	2	2	10	20	50	5	1	2	50%
Ht, nodal	8m	2m	1m	1.8m	0.4m	10cm	80 cm	10 cm	5 cm	
Resolution(HML)	H	L	H	H	L	L	L	L	L	L

COVER CLASSES: R = rare 2 = 6-15% 5 = 51-75%
(shoot not + = 1% 3 = 16-25% 6 = 76-95%
crown area!) 1 = 1-5% 4 = 26-50% 7 = 96-100%

NOTES:

TREES	SHRUBS	HERBS
H > 3m	H - Salix, Betula	H - LUAR, EPAN
M 1-3m	M - VAUL, LEPA	M - GELI, DELPHINEUM
L < 1m	L - VAVI, EMNI	L - COCA, LYCO

BOREAL PLANT COMMUNITY CLASSIFICATION PROJECT
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UNIVERSITY OF ALBERTA

RELEVÉ No. DATE JULY 6/80 FLORISTIC DATA

SPECIES	CC	CC/Ht Class (m)	Basal Area ( )						dbh ( )	
Trees		0-0.3-2.0-10-20	1	2	3	4	5	$\bar{X}$	max	$\bar{X}$
METER CLASS →		0-.3 .3-2 2-10 10-20								
Pinus contorta	3	0 0 3/8 0							11.5	
Picea glauca	+	0 +/1.5 0 0							-	
Abies lasiocarpa	1	0 1/2 +/4 0							-	

Shrubs	CC	Ht($\bar{X}$)	1	2*	3	4*	5	6	7	8	9	10	F%	ΣCCmp	$\bar{X}$C%	Rank
P. contorta	3	8 m	+	2	0	1	0	0	1	+	1	0	60	20.0	2.00	4
A. lasiocarpa	1	1.8 m	0	0	0	0	0	0	0	0	0	0	0	0.0		
B. glandulosa	+	1.0 m	0	0	0	0	0	0	0	0	0	0	0	0.0		
P. glauca	+	2.0 m	0	+	0	0	0	0	+	0	0	0	20	1.0	0.10	7
Salix sp.	2	2.0 m	0	0	0	0	0	0	+	1	+	+	40	4.5	0.45	6
E. nigrum	4	10 cm	5	2	4	3	3	3	4	4	3	3	100	287.0	28.70	1
L. palustre	1	40 cm	0	+	0	0	+	+	0	0	1	+	50	5.0	0.50	5
V. oliginosum	2	30 cm	+	2	0	2	1	+	+	1	+	+	90	28.5	2.85	3
V. vitis-idaea	1	10 cm	1	2	1	1	+	1	1	1	1	1	100	34.5	3.45	2
															1	
No. Spp. per Quadrat			4	6	2	4	4	4	6	5	6	5	$\bar{X}$ NSQ = 4.6			

COVER CLASSES: R = rare 2 = 6-15% 5 = 51-75%
+ = 1% 3 = 16-25% 6 = 76-95%
1 = 1-5% 4 = 26-50% 7 = 96-100%

NOTES: *2 2 P. contorta IN PLOT
*4 DEAD P. glauca IN PLOT

TIMBER CRUISE (5 cm prism)

	Position on Baseline at Which Cruise was Conducted				
	5 m	15 m	25 m	35 m	45 m
DBH of "IN" Trees (in cm)					
	8.5	11.5	8.5	9.5	4.5
	6.0	11.0	6.5	2.5	6.0
	8.5	5.5	10.0	8.5	3.5
	8.0	10.0	8.5	8.5	3.5
	8.5	8.0	5.0	11.0	5.5
	9.0	5.5	6.5	3.5	6.0
	8.0	8.5	4.0	5.5	8.5
	6.0	8.0	6.0	5.5	6.5
	3.5	6.0	6.0	9.0	5.5
		6.0	22.0 *	11.0	11.0
		6.5	6.0	3.5	5.0
		8.0		7.0	2.5
		8.0		5.5	8.5
		8.0		4.0	9.5
		8.5 *		8.0	3.5
		6.0			6.0
		7.0			10.0
		5.5			
		9.0*			
Mean Diameter	7.3	7.7	8.1	6.8	6.2
No. of "IN" Trees	9	19	11	15	17
Species	P.contorta	P.contorta	P.contorta	P.contorta	P.contorta
# of Border Trees	4	8	4	10	7

*Dead

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RELEVÉ No. DATE JULY 6/80 FLORISTIC DATA

Herb Species	CC	Ht ($\bar{X}$)	1	2	3	4	5*	6*	7	8	9*	10	F%	Σ CCmp	$\bar{X}$C%	Rank
C. canadensis	+	5 cm	+	1	+	1	+	+	0	1	+	+	90	12.0	1.20	1
Delphinium	+	10cm	0	0	0	+	+	+	0	0	0	0	30	1.5	0.15	5
E. angustifolium	+	30cm	0	0	0	0	0	+	0	0	0	0	10	0.5	0.05	6
G. lividum	+	12cm	0	0	0	0	1	0	0	0	0	+	20	3.5	0.35	4
L. arcticus	1	16cm	1	+	1	+	+	+	+	+	+	+	100	10.0	1.00	2.5
L. complanatum	+	6cm	0	0	0	0	0	0	0	0	2	0	10	10.0	1.00	2.5
Basidomycetes	+	3cm	0	0	0	0	0	0	0	0	+	0	10	0.5	0.05	7.5
Cladina mitis	+		1	+	0	1	+	+	+	0	0	0	60	8.0	0.80	3
Cladonia sp.	+		0	1	0	0	+	0	+	+	+	+	60	5.5	0.55	5
Stereocaulon apicum	+	2 cm	0	0	0	+	0	0	0	0	0	0	10	0.5	0.05	7.5
Nephroma	+		0	0	0	2	0	0	0	0	0	0	10	10.0	1.00	2
Peltigera	2		3	2	2	3	3	2	2	1	2	0	90	113.0	11.30	1
Mesophytic mosses	+		0	0	0	+	+	+	0	0	0	1	40	4.5	0.45	6
Pleurozium	1		1	+	0	0	1	0	0	0	0	0	30	6.5	0.65	4
NEEDLE LITTER			2	2	3	1	1	1	1	1	2	2	100			
No. Spp. per Quadrat			5	6	3	8	9	7	4	4	6	5	$\bar{X}$ NSQ =		5.7	

COVER CLASSES: R = rare; + = 1%; 1 = 1-5%; 2 = 6-15%; 3 = 16-25%; 4 = 26-50%; 5 = 51-75%; 6 = 76-95%; 7 = 96-100%

NOTES: *5 2 LOGS IN PLOT
*6 1 LOG IN PLOT
*9 DEADFALL

Appendix 2

Vegetation Observation Card

Date: Observer:

Location: Marten Activity:

Dominant Overstory Species: 10 cm d.b.h.
% canopy cover:

Dominant understory species:
% canopy cover:

Dominant shrub species:

Soil regime: Xeric Mesic Hydric

Snow conditions: depth (cm) texture

Aspect: Slope: Elevation:

Plant checklist:

Alnus crispa	*Mitella*	*Rubus cham.*
Arctostaphylos rub.	*Moneses*	*Senecio*
Carex sp.	*Pedic. lab.*	*Sphagnum*
Equisetum fluv.	*Petasites*	*Viola*
Equisetum silvat.	*Pinus cont.*	*Epilobium ang.*
Gramminae	*Poten. fruticosa*	*Clad. mitis*
Linnea borealis	*Poten. palustris*	*Clad. pod.*
Lupinus arcticus	*Pyrola*	*Clad. alp.*
Lycopodium	*Ranunculus*	*Nephroma*
Mertensia	*Rosa acic.*	
Peltigera	*Rubus arct.*	

Appendix 3

Mean catch per 100 trap nights per trapline of *C. rutilus* on 4 traplines in each habitat found in the study area during spring and fall trapping (sexes combined).

Habitat	Year	Spring	Fall
		Mean ± S.E. (n=4)	Mean ± S.E. (n=4)
I	1979	0.34 ± 0.28	0.83 ± 0.25
	1980	0.13 ± 0.04	1.63 ± 0.14
	1981	0.13 ± 0.08	
II	1979	0.59 ± 0.14	2.33 ± 0.35
	1980	0.38 ± 0.13	3.33 ± 0.35
	1981	0.46 ± 0.30	
III	1979	0.54 ± 0.14	2.29 ± 0.36
	1980	0.33 ± 0.18	2.71 ± 0.42
	1981	0.34 ± 0.15	
IV	1979	0.25 ± 0.11	0.88 ± 0.16
	1980	0.33 ± 0.12	1.50 ± 0.33
	1981	0.38 ± 0.08	
V	1979	0.38 ± 0.17	1.30 ± 0.13
	1980	0.25 ± 0.11	2.17 ± 0.49
	1981	0.29 ± 0.08	

Appendix 4

Two-way analysis of variance for the fall 1979 and 1980 trapline captures of *C. rutilus*.

Source of Variation	SS	df	MS	F	P
Treatment	350.05	9	38.89		
Habitat	325.05	4	81.26	12.07	P<0.001
Sex	8.45	1	8.45	1.26	N.S.
Interaction	5.00	4	1.25	0.19	N.S.
Error	470.75	70	6.73		
Total	820.80	79			

Appendix 5

Replicated Goodness of Fit Test (G-Statistic corrected for continuity) for the spring sex ratios.

	Heterogeneity (Gh)	Pooled (Gp)	Total (Gt)
d.f.	4	1	5
1979	7.99	1.00	8.99
1980	0.95	0.26	1.21
1981	1.28	0.24	1.52

Appendix 6

Proportion of males, based on index-trapping of habitats, for the spring trapping sessions. Sample size in parentheses.

	Habitat					
Year	I	II	III	IV	V	Pooled
1979	0.50 (8)	0.57 (14)	0.38 (13)	0.60 (5)	1.00 (9)	0.59 (49)
1980	0.67 (3)	0.70 (10)	0.50 (8)	0.38 (8)	0.67 (6)	0.57 (35)
1981	0.67 (3)	0.64 (11)	0.62 (8)	0.67 (9)	0.29 (7)	0.58 (38)

Appendix 7

Sex ratios and replicated Goodness of Fit results (G-Statistic corrected for continuity) for the summer 1980 captures of *C. rutilus* pooled over five habitats. Degrees of freedom in parentheses.

Age Class	Proportion of Males	N	G-Statistic		
			Gh	Gp	Gt
I	0.58	36	0.59(4)	0.45(1)	1.04(5)
II	0.71	24	2.04(2)	2.72(1)	4.76(3)
III	0.33	3	0.00(0)	0.00(1)	0.00(1)
IV	0.56	34	0.47(4)	0.12(1)	0.59(5)
II+III	0.67	27	2.35(2)	1.84(1)	4.18(3)

Appendix 8

Replicated Goodness of Fit Test (G-Statistic) for the sex ratios of the *C. rutilus* removed from the live-trap lines in 1980. Degrees of freedom in parentheses.

Age Class	Proportion of Males	N	G-Statistic Gh	Gp	Gt
I	0.57	72	3.42	1.13	4.54
II	0.64	120	1.91	8.64[2]	10.55
III	0.12	26	2.43	12.09[2]	14.52[1]
IV	0.47	17	0.	0.06	0.25
II+III	0.55	146	1.29	0.99	2.27

[1] $P<0.025$

[2] $P<0.005$

Appendix 9

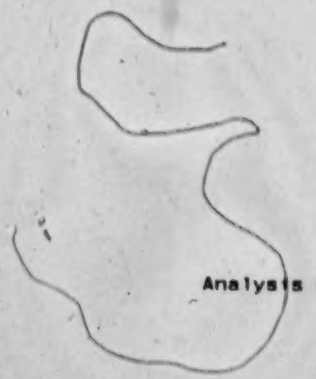
Two-way analysis of variance for the biomass of the 1979, 1980 and 1981 spring trapline captures of *C. rutilus* (sexes combined).

Source of Variation	SS	df	MS	F	P
Treatment	26938.43	14	1924.17		
Habitat	17056.35	4	4264.09	1.97	N.S.
Year	4915.31	2	2457.65	1.14	N.S.
Interaction	4966.77	8	620.85	0.29	N.S.
Error	97436.19	45	2165.25		
Total	124374.62	59			

Appendix 10

Three-way analysis of variance with replication for the biomass of the 1979 and 1980 fall trapline captures of *C. rutilus* (sexes separate).

Source of Variation		SS	df	MS	F	P
Factor A	Sex	369.80	1	369.80	0.17	N.S.
Factor B	Habitat	140136.90	4	35034.23	16.13	P<0.001
Factor C	Year	45802.02	1	45802.02	21.08	P<0.001
A X B	Sex X Habitat	6165.23	4	1541.31	0.71	N.S.
A X C	Sex X Year	2194.51	1	2194.51	1.01	N.S.
B X C	Habitat X Year	4014.19	4	1003.55	0.46	N.S.
A X B X C	Sex X Habitat X Year	135739.29	4	33934.82	15.62	P<0.001
Error		130338.72	60	2172.31		
Total		334421.95	79			



Appendix 11

Analysis of covariance for the body weights of spring-caught *C. rutilus*. Date of capture used as covariate.

1979

	df	SSx	SP	SSy	df	SSy	MSy	F
MALES								
Among Means	4	1434.60	386.11	110.72	4	6.80	1.70	0.28 N.S.
Within Groups	24	440.09	117.81	170.34	23	138.80	6.03	
Total	28	1874.69	503.92	281.06	27	145.60		
FEMALES								
Among Means	3	791.09	249.38	98.14	3	19.99	6.66	2.02 N.S.
Within Groups	16	167.71	43.20	60.58	15	49.45	3.30	
Total	19	958.80	292.58	158.73	18	69.44		

Continued.....

Appendix 11 (Continued)

1980

	df	SSx	SP	SSy	df	SSy	MSy	F
MALES								
Among Means	4	150.92	44.28	27.45	4	18.73	4.68	1.41 N.S.
Within Groups	15	3.88	5.26	53.70	14	46.56	3.33	
Total	19	154.80	49.54	81.15	18	65.30		
FEMALES								
Among Means	4	121.27	28.02	23.38	4	17.16	4.29	0.61 N.S.
Within Groups	10	2.47	1.36	63.61	9	62.85	6.98	
Total	14	123.73	29.39	86.99	13	80.01		

Continued.....

Appendix 11 (Continued)

1981

	df	SSx	SP	SSy	df	SSy	MSy	F
MALES								
Among Means	4	106.17	61.80	40.38	4	4.48	1.12	0.35 N.S.
Within Groups	17	1.33	1.10	52.64	16	51.73	3.23	
Total	21	107.50	62.90	93.02	20	56.21		
FEMALES								
Among Means	4	135.72	70.49	44.65	4	9.78	2.45	0.35 N.S.
Within Groups	11	3.28	4.13	75.04	10	69.84	6.98	
Total	15	139.00	74.63	119.69	14	79.63		

Appendix 12

Two-way analysis of variance for the body weights of the 1979 and 1980 combined fall sample of mature and immature male *C. rutilus* (early cohort).

Source of Variation	SS	df	MS	F	P
Treatment	109.60	9	12.18	2.77	P<0.01
Habitat	15.13	4	3.78	0.86	N.S.
Maturity	74.94	1	74.94	17.04	P<0.001
Interaction	21.41	4	5.35	1.22	N.S.
Error	510.28	116	4.40		
Total	619.89	125			

Appendix 13

Two-way analysis of variance for the body weights of the 1979 and 1980 combined fall sample of mature and immature female *C. rutilus* (early cohort).

Source of Variation	SS	df	MS	F	P
Treatment	2093.72	9	232.64		
Habitat	79.10	4	18.78	2.09	N.S.
Maturity	1483.75	1	1483.75	156.71	P<0.001
Interaction	61.18	4	15.29	1.62	N.S.
Error	823.74	87	9.47		
Total	2917.47	96			

Appendix 14

Two-way analysis of variance for the body weights of the 1979 and 1980 combined fall sample of *C. rutilus* (late cohort).

Source of Variation	SS	df	MS	F	P
Treatment	51.38	9	5.71		
Habitat	39.15	4	9.79	1.19	N.S.
Sex	6.36	1	6.36	0.77	N.S.
Interaction	5.87	4	1.47	0.18	N.S.
Error	1561.64	188	8.22		
Total	1613.02	197			

Appendix 15

Analysis of covariance for the body lengths of spring-caught *C. rutilus*.
Date of capture used as covariate (sexes combined).

	df	SSx	SP	SSy	df	SSy	MSy	F
1979								
Among Habitats	4	119.42	457.26	2242.39	4	1644.52	411.13	28.47
Within Groups	44	432.53	137.97	664.87	43	620.86	14.44	
Total	48	551.96	595.22	2907.27	47	2265.38		
1980								
Among Habitats	4	427.23	24.93	247.70	4	246.28	61.57	37.09
Within Groups	30	544.38	24.88	49.28	29	48.14	1.66	
Total	34	971.60	49.80	296.97	33	294.42		
1981								
Among Habitats	4	67.97	97.86	255.54	4	224.67	56.17	374.88
Within Groups	33	333.50	14.61	5.43	32	4.79	0.15	
Total	37	401.47	112.47	260.97	36	229.46		

Appendix 16

Two-way analysis of variance for the body lengths of the 1979 and 1980 combined fall sample of mature and immature male *C. rutilus* (early cohort).

Source of Variation	SS	df	MS	F	P
Treatment	174.03	9	19.34		
Habitat	41.33	4	10.33	1.12	N.S.
Maturity	73.01	1	73.01	7.91	P<0.01
Interaction	34.84	4	8.71	0.94	N.S.
Error	1079.73	117	9.23		
Total	1253.76	126			

Appendix 17

Two-way analysis of variance for the body lengths of the 1979 and 1980 combined fall sample of mature and immature female *C. rutilus* (early cohort).

Source of Variation	SS	df	MS	F	P
Treatment	3766.14	9	418.46		
Habitat	45.17	4	11.29	0.64	N.S.
Maturity	2243.74	1	2243.74	128.12	P<0.001
Interaction	141.28	4	35.22	2.02	N.S.
Error	1541.18	88	17.51		
Total	5307.32	97			

Appendix 18

Two-way analysis of variance for the condition factor of mature and immature early cohort (age classes II and III) female *C. rutilus* in the combined 1979 and 1980 fall sample.

Source of Variation	SS	df	MS	F	P
Treatment	3.081	9	0.342		
Habitat	0.178	4	0.044	2.760	P<0.05
Maturity	2.264	1	2.264	139.874	P<0.001
Interaction	0.091	4	0.022	1.419	N.S.
Error	1.408	87	0.016		
Total	4.489	96			

Appendix 19

Two-way analysis of variance for the number of litters produced by the mature age classes of *C. rutilus* in the fall trapping of 1979 and 1980.

Source of Variation	SS	df	MS	F	P
Treatment	212.80	6	35.46		
Age Class	98.53	2	49.27	2.81	N.S.
Habitat	114.27	4	28.57	1.63	N.S.
Error	140.13	8	17.52		
Total	352.93	14			